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AUTHOR: Robert Merkle DeWitt, Ph. D., 1953
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STUDIES ON THE BIOLOGY OF *PHYSA GYRINA* SAY; ECOLOGY AND LIFE HISTORY

by
Robert M. DeWitt

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Committee in charge:

Professor Frank E. Eggleton, Chairman
Associate Professor Alfred M. Elliott
Professor Felix G. Gustafson
Assistant Professor Harry W. Hann
Professor J. Speed Rogers
Associate Professor Henry van der Schalie

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The life history and ecology of Physa gyrina were studied in three ponds in Michigan. In a semi-permanent pond in southern Michigan, oviposition occurred in the spring when water temperatures reached 10 to 12 degrees Centigrade, and the adult population died shortly thereafter. Snails born in the spring may reach sexual maturity that fall, but most oviposition is delayed by low temperatures until the following spring. The life history in a semi-permanent pond 300 miles north of the above-mentioned pond differed only in that oviposition took place three to four weeks later in the spring.

Estivation forced upon snails inhabiting temporary ponds delays growth, and these rarely attain sexual maturity by the fall of the year in which they hatch. The time to reach maturity the following spring is dependent upon the length of estivation the preceding summer.

The time needed for development of the embryo varies indirectly with temperature. At room temperatures (20 - 23° C.) hatching occurred about seven days after the eggs had been laid.

Growth in P. gyrina is not determinate but continues throughout the life of the individual. Post-embryonic growth of the shell is most rapid along the longitudinal axis during

the first fourteen weeks after birth, while lateral expansion of the shell characterizes growth during the remainder of the life span. "Rest marks" on the shell were concluded not to be dependent upon environmental factors, but rather the result of a physiological pattern developed within the species.

Laboratory reared P. gyrina had a longer life span than did those living in their natural habitat, and the seasonal periodicity of oviposition, which exists in the field, had a tendency to disappear in the laboratory. A definite positive correlation existed in all snails between the length of the shell at time of oviposition, and the total number of eggs laid. In the laboratory, a high egg production appreciably shortened the individual's life. The total egg production per snail was much higher for those individuals reared in isolation than in communally raised snails, but the percentage of hatching of "virgin" eggs was much lower than in eggs produced by snails reared together. The highest percentage of hatching occurred in eggs obtained from snails collected in the field.

Physa gyrina can successfully reproduce through self-fertilization for one generation in the laboratory. The second generation reared in isolation, exhibited a great decrease in percentage of viable eggs.

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INTRODUCTION

Of the four families constituting the higher fresh-water basommatophora, the one on which the least amount of critical work has been done, is the family Physidae. The present investigation began as an attempt to study the genus Physa in Michigan. Some field and experimental work was carried on in 1940 and 1941 but the major portion was completed from 1949 to 1952. It became evident within a short time that, due to the chaotic state of the systematics within the group, the problem must necessarily be limited in its scope if any work of a truly critical nature was to be accomplished.

The confused state of affairs, which in general pervades many fields of systematics, has resulted from classifying individuals of a species as an object in an instant of time when in reality the classification should be done on the basis of their life-cycles. When the systematist speaks of a plant or animal he should be referring to its whole life-cycle, involving among other items, its morphology, reproduction, ecology, physiology and genetics. We have been too prone, in the past, when speaking of a living thing to think of it as an insect stuck upon a pin, the shell of a mollusc, the skin of a bird, or a pressed plant. Too often, the systematist who attempts to solve his problems through a study of genetics or physiology is thought to have strayed too far afield. Of necessity all aspects of an organism must be known before it can be fitted into its proper niche in a natural scheme of classification.

It is obvious, however, that an attempt to investigate all phases of biology concerning even a single species would be a task of such magnitude as to be impossible for any one individual to accomplish within his lifetime. Thus it has been necessary to confine this research to a limited number of aspects concerning the biology of Physa gyrina.

The bulk of North American investigations on the genus Physa, published by previous workers, has dealt almost exclusively with characters of shell and radula. There is extremely little material available relative to a comparative study of the soft anatomical parts and an almost complete lack of experimental investigation concerning the life history and ecology of any member of this genus.

Several lines of investigation have been pursued here. The life history has been ascertained through laboratory rearings supplemented by a field study of a selected natural population. An attempt to determine the ecological relationships of Physa gyrina was made through an extended survey of the waters in the vicinity of Ann Arbor and those of the Douglas Lake region. It is hoped that, by the combination of these various approaches, the biology of the species will be more adequately understood.

It was unfortunate that the molluscan shell - perhaps the most modifiable of structures - was utilized as the foundation upon which to build the systematics of the group. A poorer choice could hardly have been made. The layman needs but to glance briefly through the literature to realize that the search has been not for similarities between individuals

and between populations but rather a quest for differences (in many instances of a doubtful nature) that could be used to separate forms which are fundamentally the same.

A species is generally considered to be an assemblage of variants drawing their genes from a common pool and potentially capable of expressing their genetic constitution according to their gene frequency. The genetic characteristics are subject, within limits, to modifying influences of the environment which fact accounts for the variations within and between populations. Hence, to know a species we must be able to differentiate between characters which are more fluid and plastic and those which perhaps, because of their survival value to the species, are relatively stable and less subject to the molding of environmental pressures.

We must be constantly aware of the existence, in nature, of aberrant forms and of a large variety of ecophenotypes which are the responses to the effects of the environment. The ecophenotypes, present in natural populations isolated from one another, may be due to the expression or inhibition of the inherent (genetic) potential variability possessed by the entire species.

If individuals become separated from the parent population and form a new colony the probability that some genes will be lost (left behind) is very great (Diver, 1939). Inbreeding between individuals of this new colony will then produce variants that are the same as those in the parent colony except that some of the latter may have been left behind. New variations can appear only by the interjection into

the new colony of an individual or individuals from some other colony (thus changing the gene frequency) or by mutation.

The Genus Physa

Baker's (1926) proposal to raise the subgenus Physella to generic rank and thus separate the North American species of Physa from the European was based on the assumption that the nature of the mantle digitations and the extent to which they cover the external surface of the shell are of generic significance. He made this proposal in spite of an earlier publication (1901) in which he showed the extremely variable nature of the digitations, even within a species. Later, (1928) he stated that these mantle elaborations are not constant enough to serve even as specific characters. Furthermore, as far as can be determined, Baker did not base his decision to raise Physella to generic rank on a critical examination of European material. It should now be pointed out that Physa acuta, a common European species, differs markedly from P. fontinalis in that the mantle of the former is not reflected over the shell to any such extent as it is in the latter. Rather, in this respect, P. acuta approaches the condition found in P. gyrina of North America.

It might be argued that Aplexa was separated from Physa with this same mantle character serving as one of the criteria for the separation, but it is also true that Aplexa possesses other, and probably more significantly fundamental, morphological differences, especially in the reproductive system. Unfortunately, these differences seem to have been overlooked by Baker. In

contrast to these differences between Physa and Aplexa, the North American species of Physa actually closely resemble their European relatives in the anatomy of the reproductive system.

Clench (1930) does not believe that morphological differences exist between North American and European species which would justify their separation into different genera. Because of these reasons, Physa is used instead of Physella.

METHODS AND TECHNIQUES

Physa gyrina was chosen for this study as the representative species of the genus principally because of its widespread and common occurrence, its abundance, and the fact that it is easily obtainable during all seasons of the year.

Study of a Natural Population

Monthly collections of Physa gyrina were made from a selected area for a period extending through one year beginning in January and terminating in December, 1952. Throughout the year, the method of sampling was made as consistent as possible. Bottom material, composed primarily of dead willow and elm leaves, mixed with a small amount of algae, was brought into the laboratory and placed in shallow, white-enamel pans. Within 2 or 3 days all Physa gyrina were removed by hand-picking when they came to the surface of the water or crawled along edges of the pan. To insure removal of all P. gyrina, pans containing samples were kept under observation for at least one week. No attempt was made to collect the samples quantitatively but an effort was made to obtain at least 100 specimens of P. gyrina from each monthly collection.

After obtaining the samples, the snails were treated in one of two ways. Either all were first measured and specimens wanted for life history studies isolated, and the remainder fixed and preserved; or, if they were not to be used for anatomical or life history investigations, they were all dropped immediately into 70 per cent alcohol and measurements taken at

at a later date.

Two measurements, for use in growth and life history studies of the natural population, were made. These were: (1) maximum length of entire shell; and (2) greatest width perpendicular to the length. If the snails were large enough, calipers were used; if too small to be measured in this manner, an ocular micrometer was employed. The length was measured by so placing the snail that the aperture faced the observer. The shell was then turned over so that the aperture faced downward and the width determined.

Anatomical Studies

In order to secure satisfactory material both for the study of gross anatomy and for serial sections, it was found necessary to relax the snails prior to fixation. Nembutal, chloretone, alcohol and magnesium chloride were each tested as relaxing agents, but subsequently discarded in favor of menthol crystals, because the latter yielded the most satisfactory results. It was found that the best relaxation resulted when menthol crystals were powdered between the fingers and then sprinkled over the surface of the water in which the snails were located. More consistent results were obtained in this manner than by placing the snails in a saturated aqueous solution of menthol, because the latter procedure frequently resulted in the secretion of large quantities of mucus. It was noted that the extent of relaxation with menthol, and the time needed for it, varied considerably between individuals and also between samples collected at different times. In some,

anesthetization was accomplished within two hours while others that remained in the menthol solution 24 hours still retracted within their shells when dropped into the fixative. Temperature, also, has an effect upon anesthetization. Snails, placed in water containing menthol crystals and left in a warm room (20-22° C.) were much more likely to die within a short time than those placed in a refrigerator (4-6° C.). Under such circumstances of low temperature, snails have remained in good condition for a period of 48 hours although the time needed for relaxation was considerably increased.

The material for both gross and microscopical anatomical study was fixed in a 10 per cent aqueous solution of formalin. This fixative was chosen because it gave results at least as good as others and in addition had the advantage of not destroying the shell. The relaxed snails were placed directly in the formalin and left for about 24 hours after which they were transferred to 70 per cent alcohol. To insure complete removal of the formalin, the alcohol was changed 24 hours later. If the snails were to remain in the formalin for longer than a day, as was the case when collections were made during an extended field trip, the formalin was neutralized by the addition of enough powdered lithium carbonate or calcium carbonate to leave a portion undissolved. Upon return to the laboratory the specimens were transferred to 70 per cent alcohol.

A petri dish filled with one-fourth inch of dark wax served as a tray for use in gross dissection. "Minuten-nadeln" mounted in wooden applicator sticks, BB forceps and scalpels

were used as dissecting instruments. Excellent tiny scalpels can be fashioned from the "minutin-nadeln" by grinding them down, first on a coarse carborundum stone and then polishing on a finer grade stone until they have a fine cutting edge. A dissecting fluid, covering the specimen, made up of equal parts of glycerin and 70 per cent alcohol, aided in keeping the tissues pliable. Insect pins (No. 0 and No. 1) were found useful in anchoring the specimen to the wax in the bottom of the dissecting tray. Organ systems, or portions thereof, removed for more detailed study were stored in the dissecting fluid mentioned above.

When it was desirable to dissect living material, a physiological salt solution developed by Carriker (Fraser, 1946) was used to cover the snail, which had first been anesthetized with menthol. The shell was then picked away with forceps leaving the soft parts of the body exposed for dissection.

Serial sections of both the entire animal and excised organs and systems were prepared. The removal of the shell by the use of acid alcohol was invariably attended by the trapping of gas bubbles within the mantle cavity and consequent poor infiltration. This difficulty was overcome by placing the container with the snails in the acid alcohol in a vacuum desiccator attached to a vacuum pump. The snails were kept in this low-pressure chamber until the shell had disappeared. This technique usually resulted in all gas bubbles being removed from the snail's body. Standard procedures were followed for dehydration and infiltration. The

material was sectioned at ten to fifteen microns, stained in Harris' hematoxylin and Orange G and mounted in clarite. Radulae were prepared by macerating the buccal mass in 10 per cent potassium hydroxide and staining the radula with a one per cent solution of silver nitrate.

Culturing

Experimental life-history data were obtained by observing snails reared in one gallon glass jars. A hole was punched through the metal top of the jar in order to pass an air hose bearing an air-breaker into the water, which thereby was kept constantly aerated. Tap water which had been aerated for at least 24 hours was used in all rearings. Powdered calcium carbonate was added to the water to neutralize acidity and to serve as a source of calcium which might be necessary to the normal metabolism of the snail. The water in the aquaria was changed at infrequent intervals when it became cloudy or too great a quantity of fecal material had accumulated. A constant supply of food in the form of small pieces of lettuce was available at all times. Care was exercised to avoid an over-abundance of food, which, when it decayed, caused the water to become foul.

ECOLOGY

With the exception of the Ellobiidae, the basommatophoran pulmonates occur primarily in fresh waters. These habitats range from the comparatively stable, large lakes to ephemeral vernal and autumnal ponds. The requisite periods of time in which to complete the life cycle exhibit an amazing variation throughout the range of habitats. Climate too, plays a major role in determining the time limit imposed upon a species during which its life history must be completed. Thus a species living in fresh water in the temperate zone would be forced to adjust to a set of ecological factors quite different from those of a species found in tropical lakes and streams. Temperature ranges between habitats within a given geographic region may be remarkably different. In the temperate zones, larger bodies of water maintain a far more constant temperature, seasonally as well as diurnally, than do temporary ponds. Even within the spatial limits of a given habitat, temperature differences of at least a few degrees may exist, and these may be critical enough to influence the reproductive activity not only within but also between species. Physa gyrina living in a stream in Illinois which was fed by warm waste waters from a corn-products plant oviposited continuously throughout the year (Agersborg, 1932) thus differing markedly in the breeding pattern from members of the same species living in more nearly natural habitats.

The migrations of the primitive pulmonates from the sea into two distinctly new habitats, terrestrial and fresh-water, were accompanied by problems of adaptation which were not as

diverse as might appear at first glance. After the initial physiological adjustment to differences in osmotic pressures had been completed, the gastropods had a greater degree of freedom of movement within littoral and estuarine waters. In the littoral zones, where they were subjected to changes in the water level, morphological modifications evolved which allowed air to be taken into the mantle-cavity and thus the snails were slowly divorced from obligatory aquatic respiration. Once the means for aerial breathing had been acquired, the movement onto land was a relatively easy matter. Even the land pulmonates of today, however, are not entirely independent of water. The respiratory surfaces must be kept constantly moist. This is accomplished by a mucus secretion covering the epithelial surfaces and accounts for the fact that these snails are active only in a humid environment. Nor are all of the basommatophoran pulmonates entirely dependent upon the atmosphere as a direct source of oxygen. For instance, in the families Planorbidae and Ancylidae secondary gills have appeared which are not homologous to the gills of prosobranchs but are developed from anal lobes (Hubendick, 1947). The presence of the respiratory pigment, hemoglobin, within the Planorbidae enables them to obtain the necessary oxygen at lower tensions than is possible for the other groups of basommatophorans possessing hemocyanin. Instances of planorbids or ancylids having been observed in the process of breathing atmospheric oxygen are rather rare. Such is not the case, however, in Physidae and Lymnaeidae. In these groups the general practice is to depend upon a supply of oxygen coming

directly from the atmosphere. It is a common sight to see members of these families gliding on the underside of the surface film with the pneumostome breaking the film to take in a "lungfull" of air. But even within these families certain species are able to live completely submerged throughout their life (Cheatum, 1934; Noland and Reichel, 1943; Roszkowski, 1914), while others are so dependent upon atmospheric oxygen that if they are denied access to the surface they can survive only a few hours. Temperature is important in determining the oxygen demand of individuals. Physa gyrina kept in a refrigerator at four to five degrees centigrade remain inactive and rarely come to the surface. Similar behavior occurs in nature during the winter months when the water in which they are living is covered with ice. Respiratory behavior has been modified to some extent in the snails kept in aerated aquaria at room temperatures. Instead of always coming to the surface for air, they sometimes crawl over the air-breaker, extend the tube-like pneumostome and take air bubbles into the pulmonary chamber from the aerator.

It has been demonstrated experimentally that Lymnaeidae and Physidae can tolerate anaerobic conditions but to a lesser degree than Planorbidae (VonBrand, Baernstein and Mehlman, 1950). Members of these three families are commonly associated in pond communities. Physa gyrina and Lymnaea palustris have been recovered alive from bottom deposits in temporary ponds under winter conditions when hydrogen sulfide was present in such quantities that its odor was detected as soon as the ice cover had been broken. Analysis of water collected immediately

under the ice showed 3.2 ppm. of free oxygen. The quantity of dissolved oxygen would steadily decrease as the bottom of the pond was approached.

That temperature is a factor determining the length of time snails can survive experimental anaerobic conditions has been demonstrated by Alsterberg (1930). He found that snails kept anaerobically at from 0-10 degrees Centigrade lived three times as long as those kept at 20 degrees.

Natural anaerobic conditions are probably more frequently found in temporary waters than in lakes and streams. However, chemical and physical factors are so varied within a given pond, or similar habitat, that snails which are able to move from one microhabitat to another quite possibly do not have to undergo an extended period during which free oxygen is not available.

Physa gyrina is typically confined to waters of a temporary or semi-permanent nature. Stringent demands are brought to bear on the animals living in such habitats. Extreme variations in the water level, ranging from complete dryness to the maximum level for a particular pond, a wide range in seasonal and diurnal temperature, a food supply more or less limited and modified from that of more permanent waters, winter stagnation conditions which are unusually severe - all of these factors combined act as a strong selective agent which operates in modifying the species. It is remarkable that these habitats, although relatively poor in number of species, do support, on the whole, large numbers of individuals.

Fluctuations of water level and the foregoing associated

phenomena in temporary ponds have been instrumental in developing a temporal compression of the early portion of the reproductive cycle from oviposition to hatching, not only of Physa gyrina but of other species as well. Although ponds of the Ann Arbor area are usually filled with water by late fall, the water temperature at that time is normally not sufficiently high for P. gyrina to begin oviposition. From evidence assembled in the field and laboratory, the temperature at which egg-laying begins is approximately 10-12 degrees Centigrade. Thus snails of this species, which are sexually mature in the late fall, as is evidenced by the fact that they begin to oviposit immediately if brought into the laboratory at this time, on the other hand do not begin to oviposit in nature until spring. Then within the short space of four weeks, the entire reproductive cycle is completed.

In vernal-autumnal ponds Physa gyrina must endure an extensive period, sometimes lasting for six months, when water is absent from the pond and the bottom becomes extremely dry. Several means by which pulmonates living in habitats subjected to periodic drying can survive have been reported in the literature. H. B. Baker (1914) suggested that the egg masses of Lymnaea palustris and Aplexa hypnorum are able to resist dessication. He reported that no living snails were found in the dried bottom muds of the ponds he investigated but large numbers of juveniles appeared during the next rainy season. This was not true in Kenk's Pond II where immature L. palustris and Physa gyrina were estivating in dry bottom materials. Although no epiphragm was observed in any P. gyrina taken during

a dry season, such a structure has been reported in L. palustris (Mozley, 1932).

In a study of Gyraulus parvus inhabiting a temporary pond in Illinois, Strandine (1941) found that the presence of an algal mat conserved soil moisture and provided an environment which was favorable to the survival of these snails. Cheatum (1934) found the resistance of temporary pond species to dessication to be greater than that of lake pulmonates.

Although snails of temporary ponds are unable to survive complete dessication their existence in such habitats is evidence that the environment does afford sufficient moisture during periods of drought to enable hardier individuals to survive and restock the pond when it becomes filled again.

Variations between populations of P. gyrina in temporary ponds geographically isolated from one another may be due, in part, to the fact that during periods of dryness the ponds lose a major portion of their fauna, and a relatively few individuals restock the pond. The chances that members of other populations would migrate or be carried in some manner into the isolated areas are slight. Thus a population would result which had lost some of the genes present in preceding generations in that pond.

Much of the food supply in temporary ponds is allochthonous in nature and is mainly derived from terrestrial plants. This is not true in the more permanent waters which support a flora partly composed of aquatic flowering plants. The diet of Physa gyrina is composed principally of dead and decaying vegetation supplemented by the addition of living algae and water

molds. Animal remains, although eaten at times, constitute a minor portion of the diet. A liberal supply of organic matter in the form of dead leaves is available in those ponds found in a wooded area; those located in more open regions frequently have a portion of their borders lined with such plants as Typha whose leaves when dead and submerged form a favorable substrate for the growth of algae and water molds upon which the snails browse. In addition, grasses and other herbaceous plants invade the bottom of the pond during the dry season and subsequently furnish quantities of dead plant material when the ponds become filled in the fall. Ponds that are semi-permanent are much more likely to support a true aquatic vegetation which supplements the other sources of food.

Description of a Temporary Pond

The pond studied over a period of two years during this investigation was first described by Kenk (1949) and designated as Pond II. It is temporary in nature, typically dry by mid-June and fills again in late November. It is located on the west side of U. S. Highway 23 in an open grassy area about five and one-half miles southeast of Ann Arbor, and is bounded on its west side by a low elevation. The north and west margins are bordered by a growth of Typha which extends, in places, as far as five feet out from shore. A few willows and poplars grow on the northern border. Since 1941, when Kenk studied the pond, the Typha bed has increased considerably in size. The bottom of the pond is covered with a layer of brown, peaty, plant remains one to two inches thick underlaid with a clay soil.

Physico-chemical analyses were made by Kenk in 1941. Beginning on December 9 and extending through March 20, while ice covered the surface, Kenk found that the pH ranged from 5.9 in December to 6.6 in March. The dissolved oxygen, on December 9, was 11.1 ppm ; it reached a low of 1.5 ppm on January 31, and the water had a foul odor (due to decaying vegetation). Total alkalinity as determined with methyl orange measured 12 ppm on December 9, reached a high of 80 ppm on January 31, and dropped to 30 ppm on March 20.

After the ice cover had disappeared in April, the pH gradually approached the basic side of the scale, rising to 7.7 on April 15. During late April and the month of May, it dropped to 7.2 and reached a low of 6.8 on June 10, the date of the last analysis. The amount of free dissolved oxygen ranged from 3.9 to 8.0 ppm during the same period but showed no gradual increase or decrease during this time. However, no data are available as to the time of day, the depth, or the amount of surface disturbance created by wind when the oxygen samples were taken. Methyl orange alkalinity varied from 3 to 20 ppm during this period and showed a correlation with changes in pH. These measurements emphasize the instability of the temporary pond habitat.

The molluscan association of Kenk's Pond II is typical of temporary ponds in this region (Goodrich, 1932). The following species, reported by Kenk (1949) from this pond, were collected there during this investigation.

Molluscan Fauna of Kenk Pond II

Gastropoda	Pelecypoda
Lymnaea palustris (O. F. Müller)	Musculium truncatum (Linsley)
Physa gyrina Say	
Helisoma trivolvis (Say)	
Gyraulus parvus (Say)	
Planorbula armigera (Say)	

In addition to the above aquatic species, the terrestrial pulmonates, Deroceras laeve (Müller) and Succinea avara Say, were taken alive in large numbers from beneath the surface of the water in this pond. These land snails are never typical in such situations during the summer. During this study, they were present in this pond on March 6, 1951, at which time the ice cover had disappeared and the water temperature was 7 degrees Centigrade. The collection, at this time, also yielded several P. gyrina of immature size.

The pond was revisited on January 5, 1952, when eight inches of ice covered it. The water had a foul odor due to hydrogen sulfide, and the temperature was 2 degrees Centigrade. Only a few juvenile P. gyrina were taken from the sample of bottom materials on this date, the largest measuring 5 mm. in length.

The fact that the pond is, at times, without water during the winter months is probably a major factor in reducing the size of the population. Kenk reported such a case during the winter of 1944-45. Again, in the winter of 1950-51 standing water was not present until late in January. Although P. gyrina

were present in March of 1951 they were relatively scarce as compared to the preceding year when the pond was filled in November.

In April, when the temperature of the water has risen to at least 10 degrees Centigrade, P. gyrina begins to oviposit. The eggs hatch in from eight to ten days. The juveniles feed continuously and, as the pond begins to dry, move toward the center where water remains longest. By the time all the standing water has disappeared, they have burrowed into the relatively soft bottom where they remain immature until the fall rains again fill the pond. Then the snails come out of the bottom deposits, begin to move about and feed. As the water temperature drops again they become increasingly less active, moving very slowly under the ice or remaining motionless for long periods of time. Obviously, growth occurs during the winter months because mature snails, which are scarce in the fall, predominate in spring collections. Although such habitats are not optimum for P. gyrina, nevertheless these snails have succeeded remarkably well in adapting and maintaining themselves in many such temporary ponds.

Scio Habitat

This pond was chosen for study of a natural population since, being semi-permanent, it affords a year-around habitat in which Physa gyrina may continue its normal activities without interruption as was the case in the vernal-autumnal pond.

Located about eight and one-half miles northwest of Ann Arbor on Zeeb Road near the Huron River Drive, the pond is a

remnant of an old artificial channel of the river. While under investigation, the eastern portion of the pond was always joined to the river. At high water levels, during late fall and spring, the pond is of maximum size - approximately 150 feet long and 30 feet wide, the deepest portion being about 4 feet. From late July to early October, at low water, a shallow area extending across the pond from north to south is exposed, thus separating the habitat into two portions; one, at the western end, no longer in communication with the river, and an eastern part into which river water still passes freely. The isolated portion, measuring approximately 12 by 20 feet and one foot in depth during the driest period of the year, is never without water which apparently seeps into it from the river whose bed is slightly higher than that of the pond.

The pond is rather densely shaded by a large number of elms and willows mixed with a few maples. In contrast with Kenk's Pond II, no Typha is present in any portion of the habitat, nor is that part of the bottom exposed during the dry season invaded by herbaceous plants. A sparse growth of Sagittaria occurs in both portions of the pond, which are never completely dry. By far the most abundant aquatic vegetation is filamentous algae, which grows in large masses. The bottom of the western portion is thickly covered with leaves, mostly elm and willow, under which lies a layer of black muck mixed with brown peaty material. The bottom of the eastern portion of the pond, subjected to action of river currents, is relatively free from accumulated plant debris and

consists of muddy sand, coarse gravel, cobble stones and boulders. The population of P. gyrina is confined largely to the western, more sheltered portion where the water is relatively quiet and a more abundant supply of food is present.

The molluscan fauna is quite different from the association found in a temporary pond. This is due to the fact that the river species have access to the pond. Both typical river forms and those associated with backwaters are found here.

Molluscan Association of Scio Habitat

Gastropoda

Streptoneura

Campeloma decisum (Say) - abundant

Valvata tricarinata (Say) - common

Amnicola limosa (Say) - common

Amnicola lustrica Pilsbry - common

Pulmonata

Lymnaea palustris Müller - common

Lymnaea obrussa Say - abundant

Lymnaea humilis Say - common

Physa gyrina Say - abundant

Helisoma trivolvis (Say) - common

Planorbula armigera (Say) - common

Ferrissia rivularis (Say) - rare

Deroceras laeve (Müller) - rare

Pelecypoda

Pisidium fallax Sterki - rare

Pisidium compressum Prime - rare

Pisidium casertanum (Poli) - common

Sphaerium striatinum (Lamarck) - rare

Sphaerium (Musculium) lacustre (Muller) - rare

Sphaerium (Musculium) truncatum (Linsley) - common

Sphaerium (Musculium) securis (?) Prime - all immature specimens

(The Sphaeriidae were identified by H. B. Herrington.)

Operculate snails are not found in temporary waters. The fact that this group, present in the western portion of the pond isolated from direct contact with the river from latter July until early October, can maintain itself, is due to seepage from the river into this area.

In a river, Campeloma is ordinarily present in largest numbers along reaches where, due to slow moving currents, silt has been rather heavily deposited. The particular habitat in the pond at Scio meets these requirements and a large population has established itself.

The presence of two species of Amnicola is not surprising, for although members of this genus never inhabit a temporary aquatic situation, they are, on the other hand, tolerant of a wide variety of natural habitats, being found in creeks, rivers, and fresh- and brackish-water lakes (Berry, 1943). Valvata tricarinata too, has been reported from a diversity of habitats (Baker, 1928) and during this investigation has been encountered in a variety of permanent waters.

Although the Scio habitat is more or less permanent, it possesses many of the features of a temporary pond. L. palustris, P. gyrina, H. trivolvis and P. armigera are ordinarily found

together in temporary waters. L. obrussa and L. humilis are frequently found in association with these other species. Temporality of habitat is certainly not a requisite for completion of the life cycle of these animals, rather it is a factor to which they have successfully adapted, and it is not at all surprising to find this typical assemblage here.

It should be noted that such typical swift-water forms as Ferrissia are rare here, and their presence is probably accidental.

The occurrence of a terrestrial gastropod, Deroceras laeve, was noted because this species has consistently appeared in winter collections taken from beneath the ice. The slugs may have trapped as water rose in late fall. However, the fact that they are able to survive when submerged for several months, and also Pearl's (1902) report that Deroceras laeve (= Agriolimax campestris) crawl into water as the temperature is lowered and leave it as the temperature rises, leads one to believe that the presence of this terrestrial form may not be entirely accidental.

Life Cycle of Physa gyrina in Scio Pond

Field observations and collections of P. gyrina were made in the western portion of the pond, which is subject to the greatest fluctuations of water level, but which supports the largest concentration of P. gyrina. The statistical analysis of the population will be treated in a separate section.

The pond was first visited on January 15, 1952, when it was covered by ice 12 inches thick. Water passed freely

between the pond and river. Collections made at a depth of two feet yielded a small number of immature P. gyrina. Four days later, following a warm period, another collection was made at a depth of between three and four feet. The water temperature at that time was 1.5 degrees Centigrade. The majority of specimens taken were sexually mature as was indicated by the fact that they laid eggs a few hours after being brought into the laboratory.

On February 13, the water temperature was 2 degrees Centigrade, and the snails were still in deep water. When a collection was made on March 19, the pond was open and the river was swollen with runoff waters. The temperature of the water on that day was 3 degrees Centigrade. Snails from each of these collections laid eggs a few hours after being brought into the laboratory.

The following month (April 19) the water temperature had risen to 13 degrees Centigrade. The level had receded from the high-water mark noted in March, and the snails had moved from deep (3-4 feet) to shallower waters (2-6 inches) in the western portion of the pond. Numerous pairs were in copulation, and a large number of egg masses were deposited on dead leaves and sticks. These masses were characteristically reniform in shape and covered with bits of silt and other debris, which stuck tenaciously to the slimy outer layer of the mass, making it difficult to count the eggs.

The egg is considered to consist of the ovum and the albumin within the internal membrane. One mass contained a large number of eggs having no ova. Other eggs in the same

mass held embryos in the trochophore stage. In another mass, the eggs were bound together with a common external membrane but with each ovum, and the albumin surrounding it, possessing its own internal membrane. In instances of this sort there were two or three eggs within a common external membrane. None of the eggs at this time contained embryos beyond late trochophore. In the laboratory, about 48 hours elapse before a comparable stage of development is reached if the temperature remains about 21 degrees Centigrade. Since rate of development is directly proportional to temperature, the eggs collected in the field were judged to have been laid three or four days before they were found.

When the next collection was made on May 18, the water temperature (14° C.) was not appreciably different from that of the preceding month. The water had receded about two feet from the former shore. Contrasting strongly with conditions of the previous month, the population now was composed almost entirely of juvenile snails. Very few egg masses were noted.

During June and July the water continued to drop until August, when the western portion, previously described, was isolated from direct contact with the river. This condition continued through September. The mean size within the population continued to increase throughout the whole period. No egg masses were observed in the field after May 18, but a few adults taken in June oviposited in the laboratory. Snails collected in August were within a size range comparable to the previously observed ovipositing snails, and although no egg masses were observed in the field, some of the animals sub-

sequently laid eggs in the laboratory. During these four months (June - September) the water temperature remained relatively constant, dropping from 22 to 19 degrees Centigrade.

The isolated portion of the pond became flooded in October, and the water continued to rise steadily until mid-December. Increase in amount of water acted as a dilution factor and made collection of snails in adequate numbers a difficult task. The temperature dropped from 14 degrees Centigrade in October to 2 degrees in December, when a thin scum of ice covered the pond's surface. The samples taken consisted primarily of adults, and although no egg masses were observed in the field, a few were laid by snails brought into the laboratory.

Egg masses had been present in the field in large numbers in the preceding April when the population consisted almost exclusively of adults. Very few masses were present in May, and the population was made up of juveniles with only a few individuals of, or near, adult size. These facts agree with the laboratory observation that the snails begin to oviposit with an initial production of masses numbering as many as 4 per snail in 24 hours. This primary burst of activity gradually declines until several days elapse between each oviposition and it finally ceases. The individual dies a short time thereafter. Even though no masses were observed in the field during months other than April and May, the presence of small numbers of immature individuals in samples taken during months when the water temperature was above 12 degrees Centi-

grade indicates that some snails were laying eggs during that period. The certainty of the presence of sexually mature individuals in the natural population is attested by the fact that some of the snails which were brought into the laboratory during these months laid eggs.

The relatively few juveniles in collections made from November through April can be accounted for by the fact that, even though water temperature during this time was too low for snails to oviposit, these young had been hatched from eggs laid during or prior to October and growth had been retarded by prevailing low temperatures. These individuals would not mature until after April or May, and thus the appearance of young snails in the population following the latter month is not difficult to explain.

Black River Pond

This pond, a backwater of the Black River, is located in Cheboygan County about 300 miles north of Ann Arbor. In many respects it is similar to the Scio locality. It was first visited on May 17, 1951, when a collection of mature Physa gyrina was made. At this time, large numbers of egg masses were observed on submerged vegetation, and many snails were in copulation.

One month later (June 26) the population was radically changed; juveniles predominated and only very few snails of mature size were taken. No egg masses were found. Subsequent visits during the months of June, July and August yielded a series of P. gyrina which showed an increase in size each month.

Comparison of Life Cycles in Different Habitats

In the Scio habitat, the critical factor initiating and controlling reproduction of *Physa gyrina* is temperature. The phenological period extends approximately over a month after which the adult animals die.

Snails hatching in the spring become sexually mature in the fall of the same year, although they have not reached maximum size. Due to low temperatures, most oviposition is delayed until the following spring. The life span of individuals, in the field, is from twelve to thirteen months (Plate 1).

There is a smaller summer generation produced by parents which were, themselves, born during the spring of the same year. Thus juveniles and adults appear throughout a twelve-month period, adults predominating from August through April and immatures constituting the bulk of the population during the remaining months.

The population of Black River Pond followed the same general pattern as that of Scio Pond. The major difference was that the snails in Black River began their reproductive activity about one month later than did those 300 miles south. This can be accounted for by the difference in mean monthly temperatures between the two areas.

The life history of snails in Kenk's Pond II is somewhat different from that of the two preceding habitats due to the temporary nature of this pond. Oviposition in spring is still essentially controlled by temperature. The juveniles, born then, undergo a period of summer dryness, during which growth

ceases and other metabolic activities are slowed to a minimum until the pond fills again in late fall. If it remains dry until mid-winter or the following spring, the snails become sexually mature later in the season than is usual.

The general opinion that reproductive activity of mollusks is initiated by, and limited to, an optimum temperature range pervades much malacological literature related to life history. Only a few of the more critical studies available will be mentioned.

Campeloma rufum, an operculate inhabiting permanent waters, was found to have a parturition period extending from May to about September 1 in central Illinois and a life cycle of about three years (Van Cleave and Altringer, 1937). However, Viviparus contectoides, again in central Illinois, liberated young from February until May, while in central New York the birth period began in March and terminated in June. Males lived little more than a year, and females for about three years (Van Cleave and Lederer, 1932). These species are ovoviviparous, and the authors have suggested that copulation in V. contectoides takes place after release of marsupial young with the result that the new brood is not born until the following spring.

Egg laying in Pleurocera acuta, a river species, apparently extends over several months from April to June (Van Cleave, 1933). No data are given as to length of life.

Morrison (1932) found that Lymnaea haldemani has a life span of one year. Eggs are laid in the spring, about a month after ice leaves the lakes. The juveniles reach full size by

fall, overwinter as adults, lay eggs in the spring and die by mid-summer. Morrison stated, relative to the presence of egg masses in the field: "This indicates that egg laying is controlled by some sort of rhythm which is attendant on the arrival of more favorable conditions of growth in the spring. Temperature seems to be the controlling factor, or the immediate one at any rate."

Hoff (1937) reported that egg laying in Lymnaea parva extends over one month beginning in April, and the adult generation dies in June. The life span is from twelve and one-half to thirteen and one-half months.

In a study of another species of the same genus (L. modicella), Van Cleave (1935) concluded that there are two broods per year, a spring generation in March becomes sexually mature and produces a summer generation in July or August, which overwinters. He also believed that seasonal influences play a role in affecting the life cycle.

In general, these observations on basommatophoran pulmonates agree with Boettger's observations (1944). He states that snails born in the spring become sexually mature the following fall and cites a spring generation of Lymnaea stagnalis laying eggs in August, although they were not yet of maximum size. This was verified in the present investigation of P. gyrina when the spring generation of snails laid eggs if brought into the laboratory in the fall, but due to low temperatures laid no eggs in the field during the colder months. In the spring, as temperatures rise, oviposition begins and reaches a peak in April or May.

Boettger (loc. cit.) also emphasizes differences between life histories worked out in the field and in the laboratory, stating that snails brought in from the field maintain the normal reproductive pattern for some time. Then reproduction becomes more or less continuous, because of uniformity of the environment.

Physa gyrina in Relation to Other Animals

Fresh-water mollusks, in general, are of particular interest to parasitologists in that they serve as intermediate hosts to various families of helminths. Physa gyrina is known to be parasitized by several digenetic trematodes (Cort, 1914; Price, 1931); undoubtedly there are many more. Host-parasite relationships are poorly understood because so little is known of the biology of the animals involved. Control of the host organism can be effectively developed only if the life history of the snail is thoroughly known.

Encysted cercariae have been observed most frequently in tissues of the foot, mantle and kidney of the snail. These are a potential source of infection to animals feeding on the snails. Although there are no specific references to P. gyrina, the literature does contain numerous references to other species of this genus and many to Physa sp. reported to constitute a portion of the diet of fish, birds, frogs, turtles, crayfish and insects (Baker, 1916; Lagler, 1943). The habitat occupied by P. gyrina is not of commercial importance to fishermen and thus has not received the amount of attention as have those habitats harboring game fish.

Cercariea developing within a snail cause considerable damage to the host. Reproductive and digestive tissues are most frequently invaded. In one snail that was sectioned during this investigation, the entire ovotestis and a large portion of the hepatico-pancreas had been entirely replaced by numerous sporocysts. In a heavily infected population, parasitic castration must be an important factor in limiting the size of the colony. Only rarely did a field collection fail to shed cercariae while under observation in the laboratory. All of the snails collected in nature and subsequently sectioned showed varying degrees of infection. Damage to digestive and other tissues disrupts normal metabolic activities (Hurst, 1927), and, if severe enough, ultimately results in death of the snail.

Not only parasites, but predators as well, attack P. gyrina. Newly hatched young snails were observed being preyed upon by hydra which had been introduced into the laboratory culture with Elodea. Leeches, Glossiphonia stagnalis being the most common, were frequently found gorged with blood and attached to the mantle of the snails. When allowed to remain in an aquarium with snails, the leeches soon killed the entire population.

One natural population of P. gyrina was heavily infested with a commensal annelid, Chaetogaster sp. The worms were observed moving over the foot and head regions of the snail and within the mantle cavity or at its aperture, waving freely in the water. Eggleton (1952) has reported such an association between Chaetogaster limnaei and Amnicola limosa from Douglas

Lake. According to Stephenson (1930) the advantages of such an association seem to be mostly on the side of the worms, while receiving shelter they contribute nothing to the snail.

Discussion

Shifts occurring within the Scio population of Physa gyrina are presented in Plate 1. The graphs are based on a series of monthly collections plotted according to the percentages falling within certain class limits (Table 1).

Following oviposition and death of the parent generation in April, the population in May is composed almost exclusively of sexually immature individuals measuring from one to three millimeters in length. The disappearance of uniformity within the population during the succeeding months can be explained by existing age differences between broods laid by a single parent, a differential growth rate within a group of snails hatched from the same egg mass, and by the fact that there were present in May a small number of sexually mature individuals which laid eggs during the following months. Another generation appeared in September, the offspring of some of those snails born the preceding spring. Temperatures (Plate II) were high enough through the middle of October to permit oviposition to take place. From November to April, although oviposition ceased and growth was retarded by low temperature, there was a general shift in the population toward the upper class ranges.

The relative proportions (calculated in percentages - see Table 2) of sexually immature and mature individuals within

PLATE I

Monthly Collections of *Physa gyrina* Plotted According to the Per Cent of Individuals Falling Within Certain Size Class Limits. (The numbers represent the length of the shell in millimeters.)

PLATE I

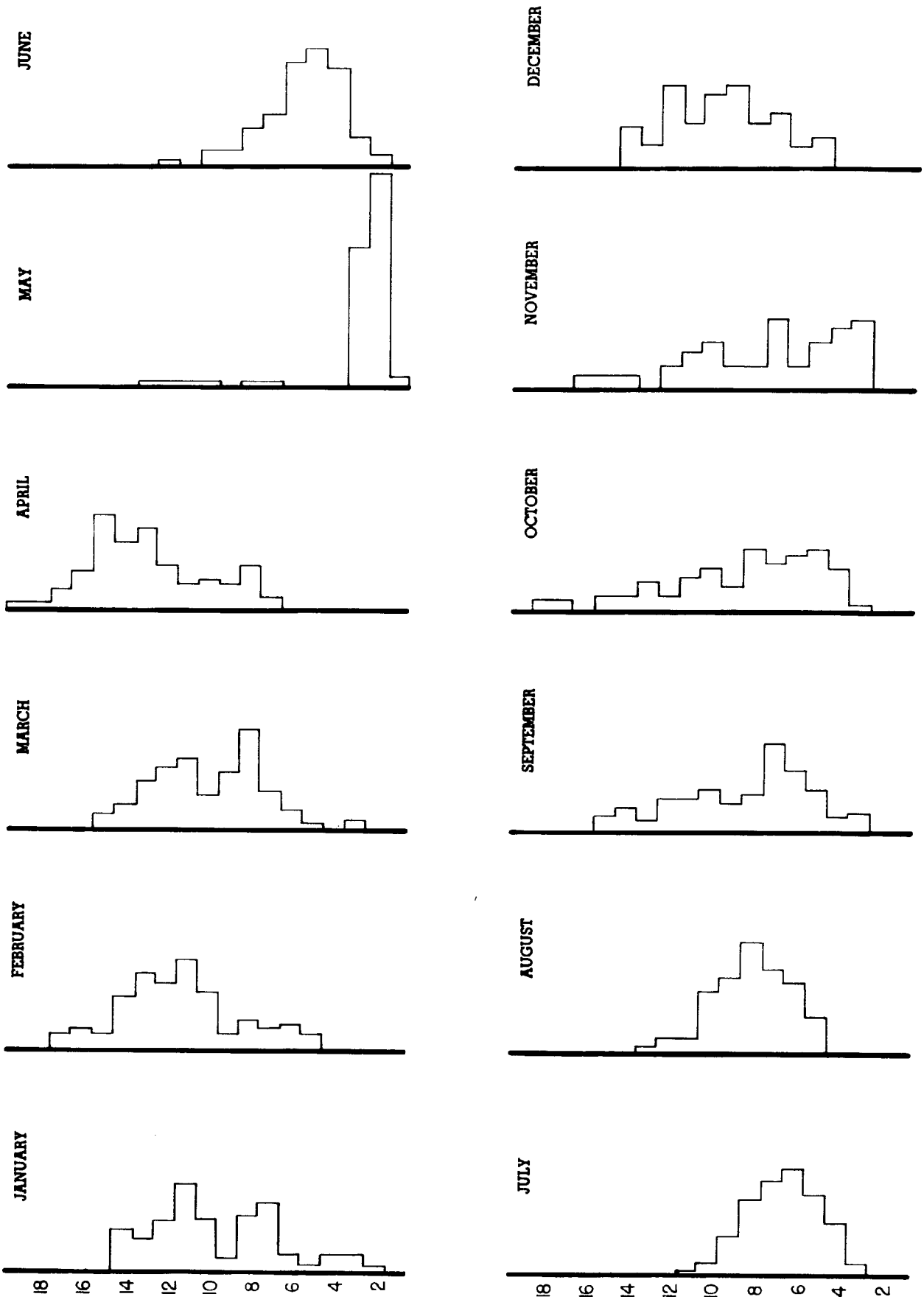
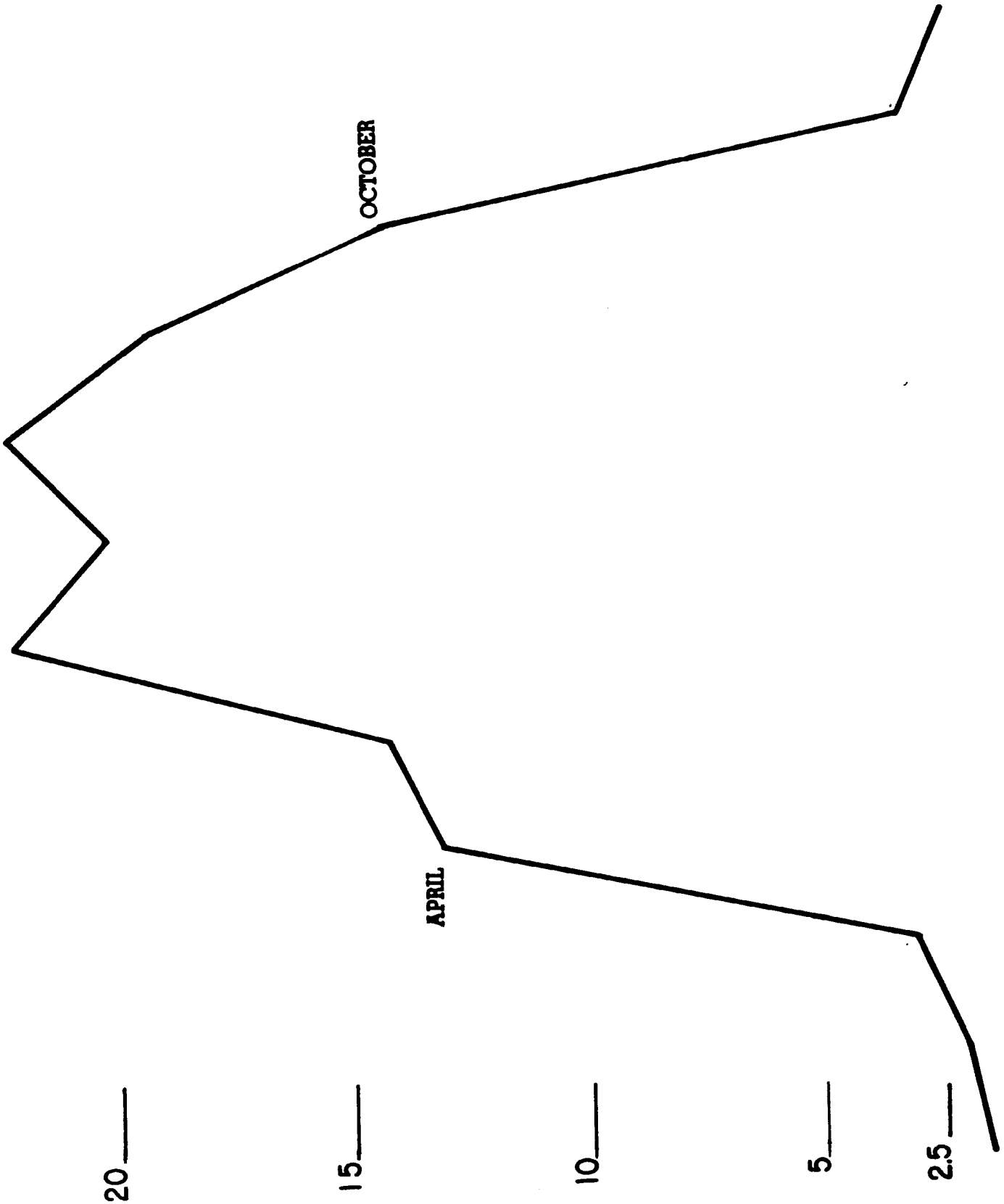

JUNE
MAY
APRIL
MARCH
FEBRUARY
JANUARY
DECEMBER
NOVEMBER
OCTOBER
SEPTEMBER
AUGUST
JULY
18
16
14
12
10
8
6
4
2

PLATE II

Temperatures at Scio (in degrees Centigrade) Extending Through a Twelve Months Period.

Oviposition did not occur below temperatures of 10 to 12 degrees Centigrade. From April to October, the temperatures were above that critical range.

PLATE II



each month's collection based on length of the specimens is shown in Plate III. Since no snail under seven millimeters in length, collected in the field or raised in isolation in the laboratory, oviposited, seven millimeters was determined to be the point below which individuals are believed to be sexually immature. Those snails seven or more millimeters in length were considered to be potentially capable of ovipositing, providing environmental factors were suitable.

Bodenheimer (1938) proposed an ecological age-classification in relation to reproduction. The life span of an individual is divided into three periods, the period of development - extending from fertilization of the egg to the first birth; the period of reproduction - lasting throughout the overt reproductive cycle; the period of post-reproduction - the time between the end of reproduction and death.

The ecological ages of the natural population of P. gyrina studied are complicated by the fact that the period of development extends from the middle of April to the middle of August (four months), by which time some of the individuals are sexually mature and engage in reproduction for as long as the temperature remains at or above the critical 10-12 degrees Centigrade (usually about two months). Between the middle of October and the middle of November, the temperature dropped below the critical value, and overt reproductive activity ceased until mid-April. This latter period of five months cannot be considered one of development nor reproduction. The vernal active reproductive period, occurring in April, is relatively short, lasting two to three weeks followed by a post-reproductive period of only a few days duration.

PLATE III

Per cent of Sexually Immature and Mature Physa gyrina Within Each Months Collection from Scio. (The numbers refer to the month in which the collection was made.)

A shell length of seven millimeters was found to be the point below which individuals are believed to be sexually immature. Those snails seven or more millimeters in length were considered to be potentially capable of ovipositing, providing environmental factors were suitable.

PLATE III

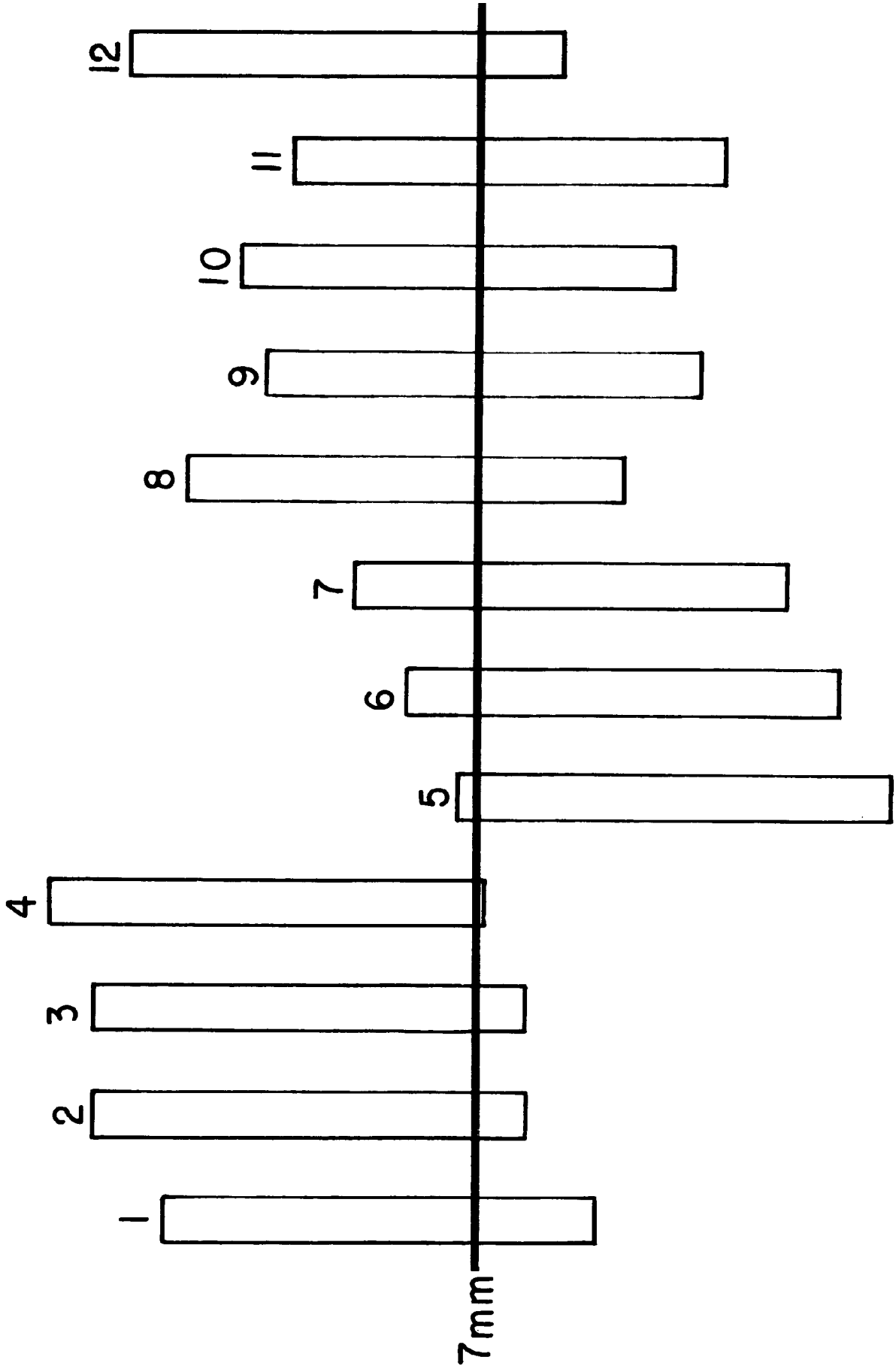


Table 1

Summary of Monthly Collections from Scio Expressed in Percentages for Each Size Group (Numbers in Parentheses Equal the Total Number of Individuals in Each Size Group)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Total Number	106	81	134	113	116	116	167	160	88	98	40	53
Length in mm.												
0 - 1					1.7 (2)							
1 - 2	0.9 (1)				62.9 (73)	1.7 (2)						
2 - 3	3.8 (4)		1.5 (2)		30.2 (35)	6.9 (8)	1.8 (3)		4.5 (4)	1.0 (1)	15.0 (6)	
3 - 4	3.8 (4)					20.7 (24)	11.4 (19)		3.4 (3)	9.2 (9)	12.5 (5)	
4 - 5	0.9 (1)	2.5 (2)	0.7 (1)			25.0 (29)	17.4 (29)	7.5 (12)	9.1 (8)	13.3 (13)	10.0 (4)	5.7 (3)
5 - 6	3.8 (4)	4.9 (4)	3.7 (5)			22.4 (26)	22.8 (38)	15.0 (24)	12.5 (11)	12.2 (12)	5.0 (2)	3.8 (2)
6 - 7	15.1 (16)	3.7 (3)	7.5 (10)	1.8 (2)	0.9 (1)	11.2 (13)	19.8 (33)	17.5 (28)	19.3 (17)	10.2 (10)	15.0 (6)	11.3 (6)
7 - 8	12.3 (13)	6.2 (5)	20.9 (28)	8.8 (10)	0.9 (1)	7.8 (9)	16.2 (27)	23.8 (38)	7.9 (7)	13.3 (13)	5.0 (2)	9.4 (5)
8 - 9	2.8 (3)	2.5 (2)	11.9 (16)	5.3 (6)		3.4 (4)	7.8 (13)	16.3 (26)	5.7 (5)	5.1 (5)	5.0 (2)	16.9 (9)
9 -10	11.3 (12)	12.3 (10)	6.7 (9)	6.2 (7)	0.9 (1)	3.4 (4)	2.4 (4)	13.1 (21)	9.1 (8)	9.2 (9)	10.0 (4)	15.1 (8)
10-11	18.9 (20)	18.5 (15)	14.9 (20)	5.3 (6)	0.9 (1)		0.6 (1)	3.1 (5)	6.8 (6)	7.1 (7)	7.5 (3)	9.4 (5)
11-12	11.3 (12)	13.6 (11)	12.7 (17)	8.8 (10)	0.9 (1)	0.9 (1)		3.1 (5)	6.8 (6)	3.1 (3)	5.0 (2)	16.9 (9)
12-13	6.6 (7)	16.0 (13)	10.4 (14)	16.8 (19)	0.9 (1)			0.6 (1)	2.3 (2)	6.1 (6)		3.8 (2)
13-14	8.5 (9)	11.1 (9)	4.5 (6)	14.2 (16)					4.5 (4)	3.1 (3)	2.5 (1)	7.5 (4)
14-15		2.5 (2)	2.9 (4)	19.5 (22)					3.4 (3)	3.1 (3)	2.5 (1)	
15-16		3.7 (3)		7.9 (9)							2.5 (1)	
16-17		2.5 (2)		3.5 (4)						2.0 (2)		
17-18				0.9 (1)						2.0 (2)		
18-19				0.9 (1)								

Table 2

Monthly Collections from Scio Grouped According to Sexual Maturity

	Under 7 mm (Sexually Immature)		Over 7 mm (Sexually Mature)	
	Number	Percentage	Number	Percentage
Jan.	30	28	76	72
Feb.	9	11	72	89
Mar.	18	13	116	87
Apr.	2	2	111	98
May	111	96	5	4
June	98	84	18	16
July	122	73	45	27
Aug.	54	34	106	66
Sept.	47	53	41	47
Oct.	45	46	53	54
Nov.	23	58	17	42
Dec.	11	21	42	79

STUDY ON REPRODUCTION

Copulation

Copulating pairs of Physa gyrina were observed in the field only during the month of April. However, snails collected from November through April soon copulated when brought into the laboratory. Since Physa gyrina is monoecious, either snail may act as a male or female but there was no indication of maleness or femaleness predominating in any one individual. This agrees with observations by Noland and Carriker (1946) on pairing in Lymnaea stagnalis.

Preparatory to copulation the "male" partner adhered to the shell of the "female" and moved to the left side of the main body whorl. The preputium was everted and withdrawn rapidly as it made probing movements in the vicinity of the female pore (located on the left side of the body posterior to the tentacle) until the penis was inserted into the genital pore of the "female." It remained there, in some instances, for as long as an hour. During this time, the vas deferens was observed to pulsate. During coitus the "female" remained quiet and its foot was turned so that it was at right angles to the long axis of the shell. The tentacles of the "male" showed no tendency to droop. Such drooping has been observed by others and explained by withdrawal of blood from the tentacles and its movement into the preputium. In one case, coitus was interrupted twice. Both times the "male" withdrew its penis and preputium within the body and about a minute elapsed before copulation was resumed. There was no evidence

of attempted self- or reciprocal-copulation, or actual chain-copulation in P. gyrina, such as was reported by Crabb (1927) in Lymnaea stagnalis.

To determine whether or not the seminal receptacle functions in storage of sperm, several snails collected in late April and early May were sectioned. Viable sperm were present in the receptacle of some individuals but were absent in others. It is possible that their absence in the latter instances was due to recent oviposition or the fact that copulation had not yet occurred.

Oviposition

In the laboratory, Physa gyrina oviposited throughout a 24 hour period but showed a definite tendency to lay egg masses during the early morning hours. Observations made on several snails while in the actual process of laying eggs demonstrated that behavior during the act is fairly consistent. The snail attached itself firmly to the wall of the aquarium with the posterior half of its foot bent sharply toward the right side of the shell. The head region was also twisted to the right. The tentacles were fully extended and the mantle digitations stood out as turgid protrubances over the right side of the shell. As the egg mass was extruded from the female genital pore on the left side of the body, the snail moved slowly in a clockwise direction. The process was completed in from ten to fifteen minutes and, each time, the snail moved immediately thereafter to the water's surface where it rested for several minutes.

Initiation of oviposition appears to be strongly influenced by temperature. Snails collected in winter and brought into the laboratory began to oviposit within two to three hours. Oviposition was suppressed by placing the snails in a refrigerator (4-5° C.) and reinitiated by exposure to room temperature (20-23° C.). The relationship between temperature and oviposition in the field has been previously discussed in the section on ecology. Using Lymnaea palustris, Cheatum (1951) demonstrated that when snails were moved from 5.5 degrees Centigrade to 16-30 degrees Centigrade there was an initial acceleration in egg-mass production which gradually returned to the normal pattern. Bretschneider (1948) reported that Lymnaea stagnalis was stimulated to oviposit by renewal of aquarium water and the addition of Hydrocharis morsus ranae (whether one factor or the other, or both, was responsible was not made clear). The length of time before egg masses were deposited varied with the temperature - production being retarded by low temperature.

In the present work on Physa gyrina, a change of water (at 20-23° C.) served to stimulate the snails to oviposit within one or two hours. However, the addition of Elodea, a member of the same family as Hydrocharis, produced no effect on the pattern of oviposition.

Van Nieuwenhaven and Lever (1946) found that the effect which Hydrocharis had upon oviposition was due to the oxygen produced by the plant and that Lymnaea had to come in contact with its leaves to be stimulated. In addition, these workers state that a great but gradual rise in temperature (from 18

to 28° C.) served as a strong stimulus to egg production.

Egg Masses

Several egg masses of Physa gyrina were examined immediately after they had been laid. They were not milky in appearance, as the masses of Physa heterostropha and Lymnaea palustris are reported to be (Bondesen, 1950), but were completely transparent.

The eggs of P. gyrina are laid embedded in a thick, clear, jelly-like mass surrounded by a sticky, tough outer layer to which particles of debris frequently adhere. In nature, the egg masses are firmly attached to leaves, stones, sticks, submerged vegetation or the shells of other snails - rarely are they floating free in the water. Masses laid in the laboratory are most frequently fastened to the sides or bottom of the container holding the snail. At times they have been taken from lettuce floating at the water's surface.

The masses are characteristically reniform in shape, the amount of curvature depending upon the number of eggs in the mass. Those with few eggs (3-5) are roundish or oval with little or no curvature. Masses containing approximately the maximum number of eggs (118) were so curved that the terminal portion of the mass met the initial part.

Sperm penetration of the ovum occurs within the snail and oögenesis is completed after oviposition. Accumulation of yolk material in one hemisphere of the ovum gives it a yellowish color and marks the vegetal pole. The animal pole has a distinctly lighter appearance and can be later identified

by the polar bodies which appear there. The ovum and a quantity of albumin around it are surrounded by an envelope, the albumin or internal membrane. Enclosing this is a series of fine lamellar structures forming the external membrane.

The egg which is considered to consist of the ovum and the albumin around it within the internal membrane contains the sole source of food available to the future embryo, until hatching. "Egg strings," formed from the external membrane and "egg designs" (a pattern impressed upon the egg) as described by Bondesen (1950) for the eggs of Physa fontinalis, were not observed in P. gyrina.

Among those snails collected in the field, or those of the first generation reared under conditions as favorable as could be produced in the laboratory, the smallest which oviposited viable eggs, was 7 mm in length. The size of the egg mass varied directly with the size of the snail at time of oviposition only in the case of the largest and the smallest individuals. No close correlation existed between dimension of masses and snail size for those snails falling between the two extremes in length.

The eggs of a single mass vary from spherical to ovoid in shape. The ovum proper is usually placed eccentrically within the egg and remains in this position until the embryo, during the trochophore stage of development, starts its revolving motion.

There is considerable variation in mean number of eggs per mass. It is highest in masses produced by snails taken in the field and lowest in snails reared together in a common aquarium (Table 7).

The mean size of a number of eggs that were measured was 0.79 by 0.72 mm. The largest of the group was 0.96 by 0.80 mm, the smallest 0.64 by 0.56 mm. Bondesen (1950) reports the size of eggs of Physa fontinalis, a European species, without the external membrane to be 1.08 by 0.75 mm; of P. heterostropha, a North American species introduced into Europe, to be 0.68 by 0.54 mm.

A number of uncleaved ova were measured. The mean diameter was 0.14 mm and the range was 0.13 to 0.15 mm. This range in size of the ova of P. gyrina is quite consistent. A series measured in 1941, produced by snails from a colony different than the ones studied later, ranged from 0.13 to 0.16 mm, the majority were 0.14 mm.

Anomalies of eggs and egg masses of P. gyrina appeared rather frequently. It has been noted that the size of the snail at hatching depends largely upon the supply of albuminus material available to the developing embryo. Abnormal development frequently occurred in very small eggs.

Another irregularity, in which two or three eggs were surrounded by a common external membrane was observed in masses laid by snails, both in the field and in the laboratory. These eggs proceeded to develop normally.

In several instances, ova were found in the terminal portion of the mass which were not enclosed in either an external or internal membrane. These ova failed to undergo the first cleavage.

Eggs surrounded by an external membrane and lying outside of but attached to an egg mass were rather common. Several

masses containing only one egg but regular in all other respects were found. Development followed a normal pattern in both of these anomalies.

Polyvitelline eggs of fresh-water snails have been the subject of investigation of several zoologists. Crabb (1931) was unable to attribute the presence of two or more ova within a single egg to any cause other than their accidental inclusion. He rejects the idea that they may have arisen as a result of the separation of the zygote into two parts during early cleavage.

Crabb's explanation is supported by these observations on the eggs of Physa gyrina. In all uncleaved ova observed, maturation had not occurred by the time of deposition and two polar bodies were seen to form shortly after the eggs were laid. This was true of eggs containing several ova as well as those in which a single ovum was present. It is highly improbable that the ovum had divided prior to maturation. Furthermore, since cleavage in mollusks is determinate, if the several ova within a single egg had arisen from a single egg cell the progeny would be expected to be mirror images of each other. Such cases were not observed by Crabb nor were any dextral Physa gyrina hatched from polyvitelline eggs. During this investigation, 51 Physa gyrina laid a total of 25,515 eggs with only 22 of them containing two or more ova.

Of the 51 individual snails studied, 10 produced polyvitelline eggs. Tur (1910) stated that some races of Philine aperata (an opisthobranch) produce polyvitelline eggs rather consistently, other races rarely or never. In this work,

individuals from two separate localities were studied. There was no indication that either population had a greater tendency to produce eggs with more than one ovum. Nor was there any indication that the production of polyvitelline eggs is influenced by heredity as was suggested by Winsor and Winsor (1932). Crabb and Crabb (1927) also concluded that the phenomenon was due to chance and not inherited.

The fact that snails taken in the field, those reared in isolation in the laboratory from stock collected from two localities, and eight individuals reared together in the laboratory all laid polyvitelline eggs indicates that environmental conditions were probably not responsible for the phenomenon.

There was a tendency for polyvitelline eggs to be included in masses laid near either the beginning or end of the period of oviposition. Masses with a small number of eggs usually contained those which were polyvitelline. Mortality was high in polyvitelline eggs; of the 22 containing 45 ova, only nine (20 per cent) of the ova developed and hatched. Five of the masses with polyvitelline eggs also contained other anomalous specimens.

Numerous eggs with more than one ovum were laid in the laboratory by Physa gyrina studied in 1941. The largest number of ova within an egg observed at that time was 13. Development proceeded as far as late cleavage when all 13 embryos died. Crabb (1931) reported an egg of P. gyrina which contained 25 ova (vitelli).

Masses in which some or all of the eggs lacked ova were

laid. Some individuals produced such eggs near the beginning of the ovipositing period, others in the middle or at the end of the period (Table 3). There was a tendency for the masses containing empty eggs to be laid in succession. Also, those snails producing the largest numbers of polyvitelline eggs laid the largest number of eggs lacking ova.

The presence of empty eggs and masses lacking eggs laid at varying times within the ovipositing period of several individuals of Physa gyrina does not agree with Colton's observation, on Lymnaea columella, that the appearance of empty eggs is a sign of senility and comes at the end of the reproductive cycle. However, these observations on P. gyrina agree with those of Forbes and Crampton (1942) made on Lymnaea palustris.

Nekrassow (1929) claimed that the shape and structure of the eggs and egg masses, as well as the number of eggs per mass and their arrangement within the mass are specific characters and should be considered in the classification of snails. Bondesen (1950) believes that the study of egg masses and their contents can furnish information on relationships existing between families and higher categories of the gastropods. He suggests, on the basis of studies of the spawning products, that the Opisthobranchia are closely related to the Pulmonata, a conclusion reached by Hubendick (1945) after a study of the comparative anatomy of these groups.

Table 3

Summary of Egg Masses Produced Containing Eggs Lacking Ova

Snail Number	Total Number Egg Masses	Total Number of: Masses with Eggs Lacking Ova	Eggs in These Masses	Eggs without Ova
23	26	2	53	3
24	30	4	191	48
1-2*	61	2	6	2
1-4	49	17	233	91
2-4	26	1	12	2
2-6	42	1	8	1
9EM6-1	73	9	79	38
9EM6-4	59	2	19	5
9EM6-6	62	4	36	12
9EM6-8	121	3	25	3

Snails 23 and 24 were collected in the field and isolated in the laboratory;

9EM6-8 was a lot of eight snails reared together in the laboratory;

The remainder were laboratory reared in isolation.

*This snail also laid four empty egg masses.

Embryological Development

Compression into the egg of the larval stages, free-living in most marine snails, is characteristic of land and fresh-water gastropods. A suggestion, commonly accepted, that accounts for the disappearance of free-living larval forms in fresh-water mollusks is that due to the weak swimming ability of the larvae and the decrease in buoyancy of fresh-water, they would likely be swept into the ocean by river currents and would not survive. Nevertheless, the presence of free-living larval forms during the life-cycle of some mollusks is not an absolute barrier to existence in fresh water. The pelecypod, Dreissenia, has such larvae and lives in fresh water.

The larval stages within the egg have been termed trochophore and veliger by Baily (1939) and others, or trochophore and post-trochophore by Lowrance (1934). Regardless of the terminology, it is possible to recognize two stages, corresponding to some extent to free-living larvae, developing within the egg of land and fresh-water snails.

The series of events in embryological development here described took place at room temperatures, which ranged from 20 to 23 degrees Centigrade. No polar bodies were present in eggs examined immediately after they had been laid. The first polar body was extruded in from 10 to 20 minutes and its appearance was followed within the next 45 minutes by the formation of the second polar body and first cleavage of the ovum. The two-celled embryos underwent the second cleavage within the next hour. At the end of the fifth hour, following

oviposition, the first quartet of micromeres had appeared. Cleavage then proceeded rapidly: the fourth, fifth and sixth divisions took place within the next 90 minutes.

The next day, 24 hours after oviposition, the trochophore stage had been reached. This stage is characterized by revolutions of the embryo which begin as jerky, irregular, slow movements, later becoming smooth, sustained, and rather rapid. A striking feature of the trochophore is the presence of a clear, bilobed vesicle, appearing in the region of what was originally the animal pole, which later coalesces to form a single lobe. This represents the future foot of the snail. The point of its appearance is marked by the polar bodies which have a tendency to remain attached at the animal pole of the embryo until they are pushed away from it by the outgrowth of the foot anlagen.

During the next 24 hours, the embryo gradually assumed the features characterizing the veliger. A mass of endodermal cells marked the position of the visceral mass. A large and rather shallow shell gland made its appearance at a point later represented by the spire of the shell. There was no evidence of the shell being present at this time.

On the fourth day, following deposition of the eggs, the veliger was well defined. The foot, formed from the bilobed anlagen present in the trochophore, was well differentiated and there was a sharp demarcation between the head-foot region and the visceral mass. Small bulges representing tentacles with darkly pigmented eyes at their bases were present. The margin of the mantle was marked by a raised ridge of cells

encircling the lower part of the visceral mass. The heart began to beat during the fourth day and the embryo exhibited considerable coordination of movement. Periodically (every 10 to 20 seconds) the visceral mass was contracted toward the head-foot region. Cilia could be seen beating around the margin of the pneumostome and the fluid within the egg circulated freely within the pulmonary chamber.

At the end of the fourth day, the miniature snail possessed all the structures found in a newly hatched individual. The characteristic foot and filiform tentacles of the Physidae and a thin, transparent, yellowish shell covering the mantle were present. The embryonic snails grew until they almost completely filled the egg at the end of the sixth day. Hatching usually began on the seventh day and by the end of the eighth all normal young snails had escaped. Although a size difference exists at time of hatching (correlated with the size of the egg) there is no definite indication that this difference continues to exist through post-embryonic life.

Young snails escaped from the egg by first rasping through the internal, and then through the external membrane. Perforation of the membranes was aided by the snail periodically thrusting its foot against the wall. The process was completed within 20 to 30 minutes during which time the snail rested frequently. After it had hatched the internal membrane of the egg collapsed. Once outside the egg, the snail moved freely in the jelly of the mass. Escape from the egg mass was made through a hole gnawed in its outer wall or through an opening made by another snail. Rather frequently young snails escaped

from the eggs and died a few days later within the egg mass jelly. They were unable, for some reason, to escape through the membrane surrounding the mass.

The time needed for development, prior to hatching, is directly proportional (within limits) to the temperature. At room temperatures of 20 to 23 degrees Centigrade, seven to eight days elapsed before all normal snails in an egg mass had escaped. This time differs greatly from Baker's (1928) report that 40 days elapsed between the time Physa gyrina hildrethiana laid eggs in the laboratory and young snails, 0.5 mm in length, were observed. Young Physa gyrina observed in this study averaged 0.8 mm in length at time of hatching. It appears that Baker failed to note the exact hatching date and as he apparently had 14 egg masses (number of eggs not stated) in the same container, growth of the young was retarded. He stated that in 12 days the young had doubled in size, measuring 1 mm in length. This does not agree with results obtained here where isolated young snails more than doubled their length in 7 days.

During the summer, when laboratory temperatures remained around 30 degrees Centigrade for two months, the time required for hatching was reduced by as much as 24 to 36 hours.

Development is considerably delayed when eggs are kept at a temperature of 4 to 5 degrees Centigrade. Two egg masses, laid by the same snail within a few hours of each other, were selected and one was kept at room temperature (20-23° C.), the other was placed in a refrigerator (4-5° C.). Observations were made daily on both masses.

The one at room temperature contained 12 eggs. Development proceeded normally and at the end of the seventh day all of the snails had hatched.

The mass in the refrigerator contained 19 eggs. At the end of the eighth day, none of the embryos had advanced beyond the gastrula, a stage ordinarily reached and passed in less than 24 hours. This same mass was moved to room temperature at this time. Three days after being removed from the refrigerator the embryos were in late trochophore and many appeared to be abnormal. Two days later, 13 of the 19 eggs contained embryos which bore little resemblance to the usual immature snails of the same age. Seven days after the mass had been taken from the refrigerator, four of the six normal immature snails had hatched. The fifth and sixth hatched on the two succeeding days. Two abnormal snails hatched, one on the tenth and another on the eleventh day. The remaining 11 embryos died.

Abnormal snails hatched from egg masses laid by a number of parents. In some the shell failed to develop, and the snail emerged from the egg naked; the heart was enormously developed in others. One snail possessed 4 eyes, 3 tentacles and had no shell. In nature these monsters would probably not hatch; if they did they would not survive. A few anomalous snails lived in the laboratory for several days although no attempt was made to rear them.

Young snails, after leaving the egg mass, rest for a short period and then move to the surface of the water. This action may be prompted by a demand for oxygen because the

pulmonary chambers of newly hatched snails are filled with fluid. After the trip to the surface the chambers are clearly outlined by a bubble of air. During this period many of the young snails crawl out of the water, become dried and die. This behavior may be due to an attempt to break through the surface film in order to obtain atmospheric oxygen.

Growth

Both embryonic and post-embryonic growth of Physa gyrina was studied in the laboratory. A series of embryos was measured at daily intervals from the time the eggs were laid until they hatched. To determine the rate and extent of post-embryonic growth, a series of snails, hatched from one egg mass, was isolated and the length and width of the shell were measured periodically from birth until death.

Embryonic growth in Physa gyrina follows the same general pattern that has been determined for most other metazoan animals. There is no appreciable increase in total size of the embryo during cleavage; as the total number of cells increase, they become smaller. Measurable increase in the mass of embryonic tissue follows gastrulation and subsequent development of the structures characterizing the trochophore. The greatest rate of growth accompanies the development of the post-trochophore at which time many of the organs found in the adult snail make their initial appearance. Following this period, the rate decreases as the young snail, within the internal membrane of the egg, nears the maximum prenatal size which is limited by

the size of the egg.

Embryonic measurements were made of the whole animal, not of a particular portion, as was done for post-embryonic growth. Growth of the embryo is not simple additive growth, such as is found in the shell, because the increment added is alive and begins to grow itself as soon as it has been produced. The increment is not independent of the amount already present but is dependent upon the latter. Hence growth of the whole embryo is by multiplication in a geometric series. Simpson and Roe (1939) have contrasted this type of growth, which they term multiplicative, to compound interest as opposed to the simple interest or additive growth of a shell.

Average geometric growth rates were calculated for two series of developing embryos using the formulation of Simpson and Roe (1939):

$$G = 2.303 \frac{\log Yt - \log Yo}{t}$$

where:

Yo = initial magnitude

Yt = magnitude at time t

t = time measured at intervals of 1 day

G = geometric growth rate

That the growth rate is not constant for each successive time period of observation is shown in Table 4. This is not only the average rate for each period, but also a series of actual rates, and thus shows the changes in rate which actually occurred.

Table 4

Mean Measurements of the Growth of Embryos

Group I contains 11 embryos; Group II 9 embryos. Column I is the stage of development of the embryo at time of measurement. Column II contains the mean absolute measurements in millimeters. Column III is the average growth rate.

	Group I			Group II		
	I	II	III	I	II	III
1st Day	Early Trochophore	0.15	---	Late cleavage	0.14	---
2nd Day	Late Trochophore	0.20	0.288	Early Trochophore	0.16	0.134
3rd Day	Post-Trochophore	0.36	0.588	Trochophore	0.23	0.363
4th Day	Well developed	0.48	0.288	Post-Trochophore	0.41	0.578
5th Day		0.64	0.288	Well developed	0.52	0.240
6th Day		0.71	0.104		0.69	0.281
7th Day	Hatched	0.83	0.156	Hatching	0.78	0.123

The eggs in Group I were laid about 8 hours earlier than those in Group II.

The shell grows by addition to pre-existing shell material. Thus the initial size of the structure is incremented by an addition which does not itself grow and which is independent of the material already present. The mean height of the shell of the six snails at the end of definite periods of time (termed mean absolute growth) is shown in Table 5 and Plate IV. The mean additive growth rate per week of the lengths of the shell of six Physa gyrina, measured over a period of a year (from birth to death), was calculated using the following relationship of Simpson and Roe (1939):

$$A = \frac{Yt - Yo}{t}$$

where:

Yo = initial magnitude

Yt = magnitude at time t

t = time measured at weekly intervals

A = additive growth rate

The data are presented in Table 5 and Plate V.

Post-embryonic growth of the shell of Physa gyrina, under natural conditions, is not a continuous process but is interrupted at intervals. These periods, during which growth ceases, are indicated on the shell by rest marks termed varicose bands.

The shell is elaborated by a glandular area of the mantle located at its free edge. A pigment deposited in the shell material as it is laid down gives it a reddish-brown color. When growth is interrupted for some reason, the inner edge of the outer lip of the aperture is strengthened by a triangular,

Table 5

Mean Growth Measurements of Six Snails Reared in Isolation

Measurement Made at End of:	Range in mm.	Absolute Growth (Length in mm.)	G Additive Growth	Obesity Index
1st Week (Born)	0.80-0.88	0.83	----	1.35
2nd Week	1.76-2.08	1.95	1.12	1.46
3rd Week	3.12-4.80	3.71	1.76	1.60
4th Week	5.75-7.50	6.54	2.83	1.74
5th Week	7.75-9.50	8.75	2.21	1.77
6th Week	9.50-10.50	10.17	1.42	1.77
8th Week	11.50-12.50	12.04	0.94	1.87
10th Week	11.75-12.75	12.25	0.10	1.87
12th Week	11.75-12.75	12.25	0.00	1.87
14th Week	11.75-13.50	12.54	0.15	1.88
16th Week	12.00-13.50	12.63	0.05	1.85
20th Week	12.25-13.50	12.79	0.04	1.84
25th Week	12.25-13.50	12.83	0.008	1.84
30th Week	12.25-13.50	12.92	0.018	1.85
52nd Week	13.00-14.00	13.63	0.032	1.84

PLATE IV

Mean Absolute Growth in *Physa Gyrina*

Growth, as indicated by height of shell, is most rapid during the first five weeks of the life of the snail. After that time, it decreases and there is only a slight increase in height following the twentieth week.

PLATE IV

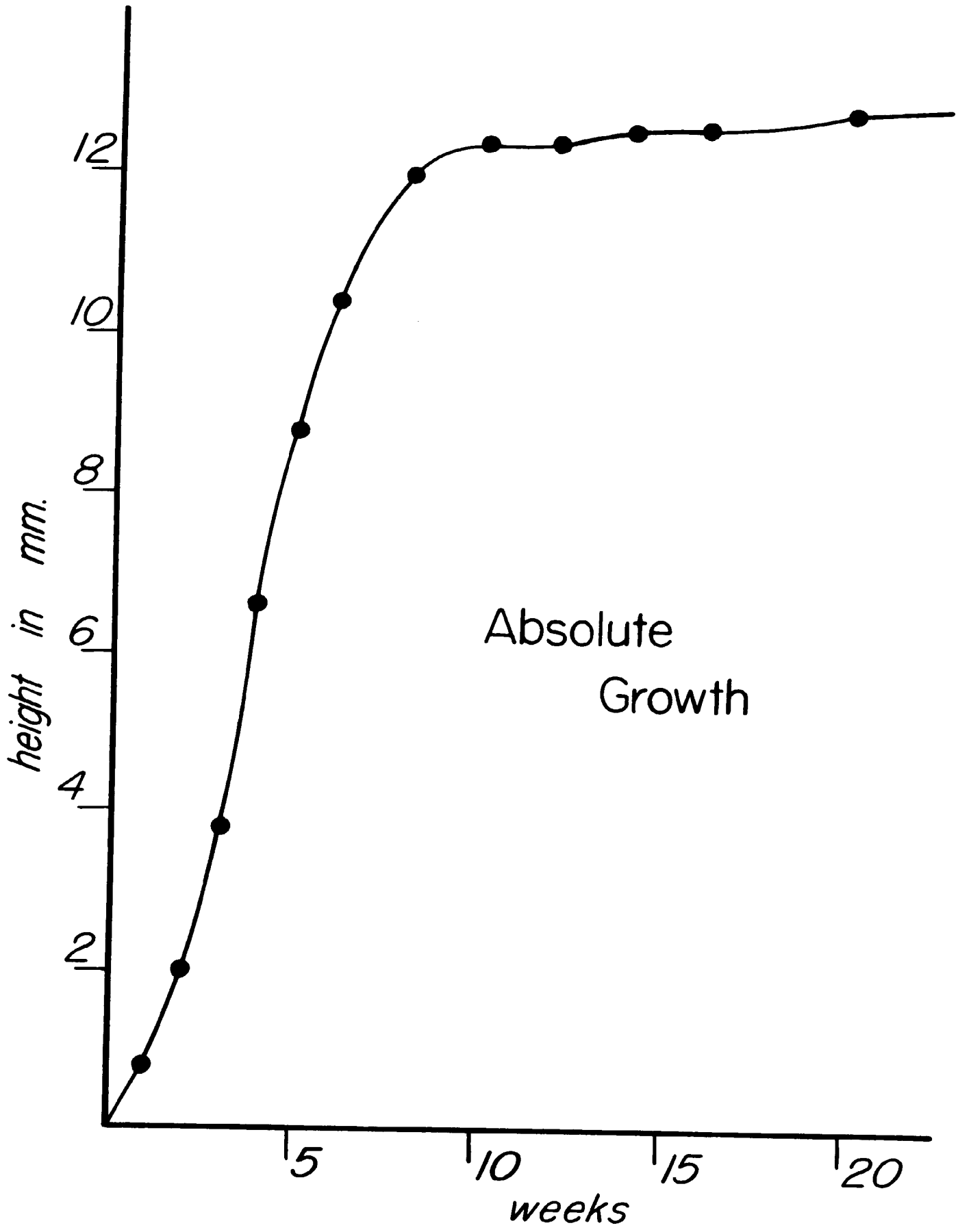
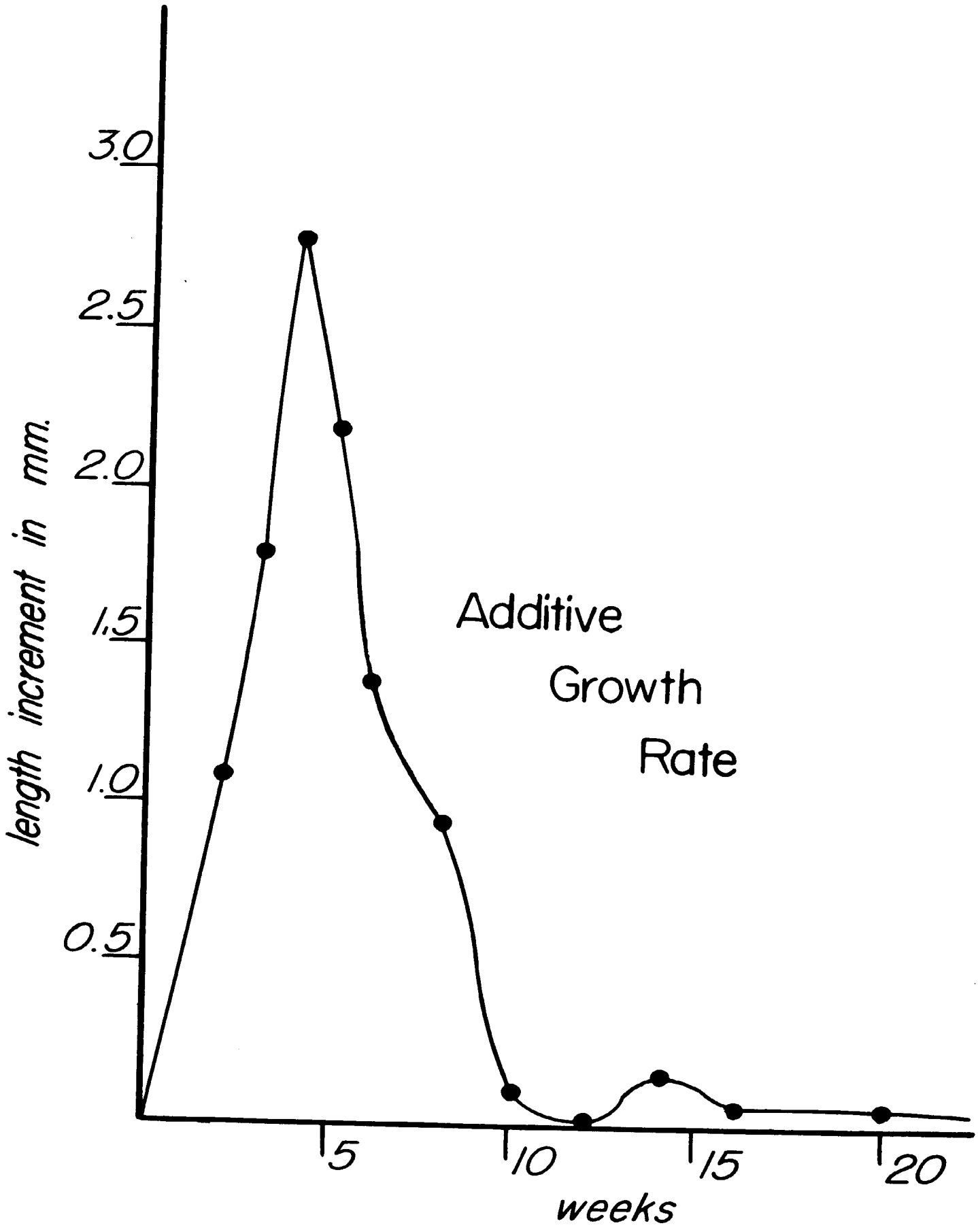


PLATE V

Additive Growth Rate of Physa Gyrina

Rate of increase in height, by addition to pre-existing shell material, is most rapid during the first five weeks. It then drops rapidly until the end of the tenth week when it levels off and remains relatively constant for the remainder of the life of the snail.

PLATE V


3.0
2.5
2.0
1.5
1.0
0.5
length increment in mm.
Additive
Growth
Rate
5
10
15
20
weeks

thickened band which contains less pigment than other portions of the shell. This varicose band may or may not be bordered on either side by a heavily pigmented stripe. Crandall (1901) attempted to use these rest marks in combination with other shell features as specific characters. He assumed that one rest mark indicated a year's growth and stated that Physa gyrina was a tri-annuan, requiring three years to reach maturity. These snails have been taken in the field with as many as six varicose bands although the majority possessed two. As was stated in the section on Ecology, P. gyrina lives from twelve to thirteen months under natural conditions.

Conditions which arrest growth and lead to formation of varicose bands are obscure. Laboratory reared snails under nearly constant environmental conditions of temperature, light, aeration and food supply had as many as three well-defined bands on the shell. The longest life-span of any one of these cultured snails was 450 days.

Interruptions of growth are to be expected in those snails living in a temporary habitat. The varicose bands on the shells might be accounted for in terms of periodic drying of the habitat but, it is difficult to imagine that a snail can produce the thickening while the pond is drying or while the animal is estivating in the dry pond. Physa gyrina living in semi-permanent waters and in laboratory cultures produce varicose bands similar in number and nature to those produced by snails living in temporary ponds. This appears to indicate that production of these bands are not dependent upon environ-

mental factors but rather are the result of a physiological pattern developed within the species and perhaps modified to some extent by environment.

Length-width ratios of the shell of P. gyrina do not remain constant from the time of hatching until the death of the individual. Failure to recognize this led such early conchologists as Tryon to describe as a new species, immature forms of P. gyrina (Baker, 1910; Clench, 1925). Baker's (1902) statement that Physa gyrina is dimorphic, short- and long-spired forms being present within the species, was due to his failure to recognize the presence of different age groups within a population at any one time. He stated relative to short- and long-spired forms of P. sayii, "were it not for the closely connecting individuals, the short-spiral form would be worthy of varietal distinction."

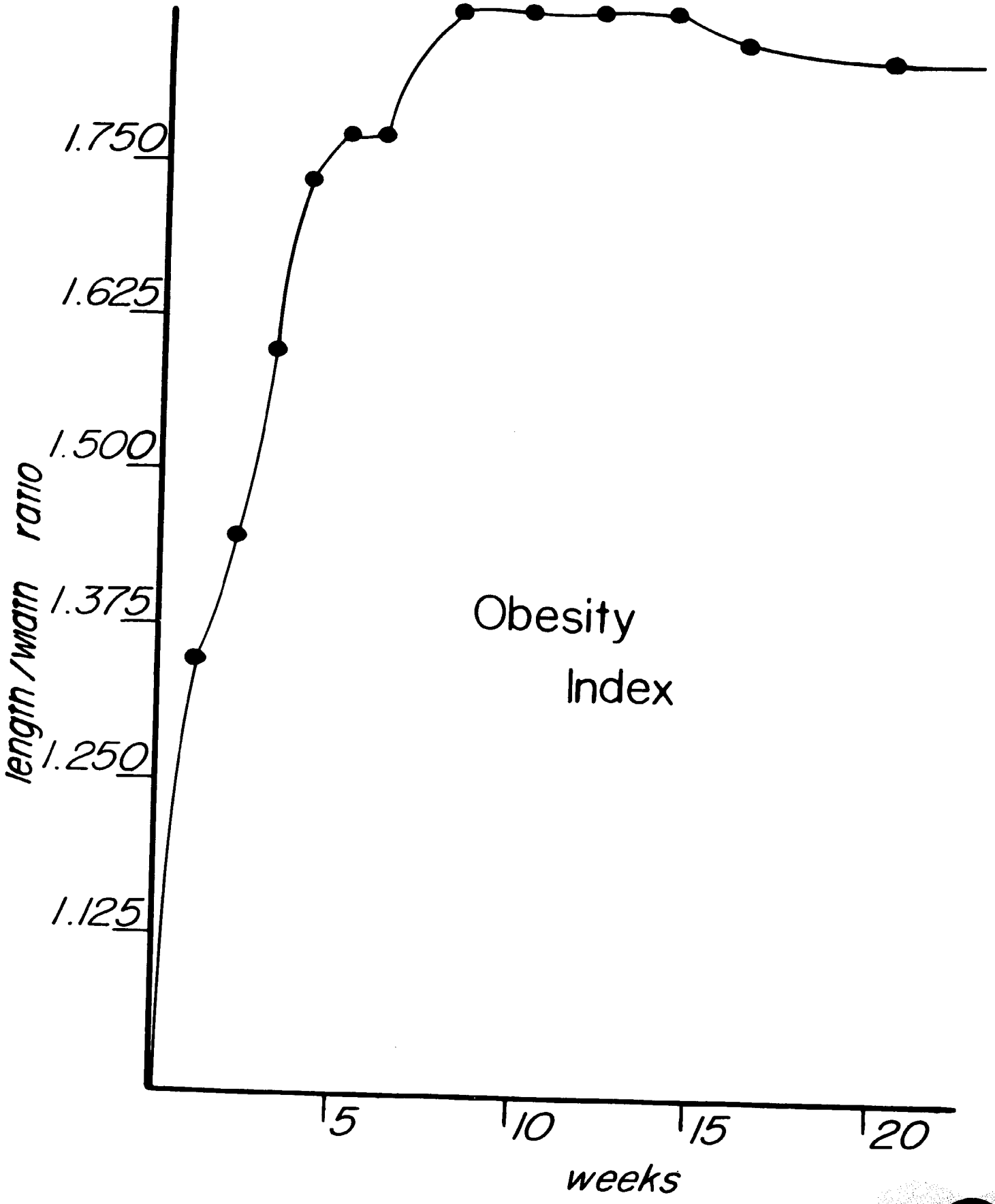
Measurements of the length and width of the shell were made on six snails over a period of a year and showed that the obesity index, calculated by dividing the length by the width of the shell increased through the fourteenth week and then gradually dropped and leveled off for the remainder of the life span (Plate VI). During the first portion of the cycle, the shell grew most rapidly in a longitudinal direction. The slight drop in value of the obesity index indicated that, although a small amount of growth occurred, it was in a lateral direction - that is, there was a noticeable flaring of the outer lip of the shell. These observations on Physa gyrina generally agree with those Crabb (1929) made on Lymnaea stagnalis.

PLATE VI

Obesity Index of *Physa Gyrina*

The index was calculated by dividing the height by the width of the shell. The rapid rise during the first seven weeks indicates that the shell was growing more rapidly along the longitudinal than the lateral axis. Following the fourteenth week, growth was largely confined to a lateral expansion.

PLATE VI


1.750
1.625
1.500
1.375
1.250
1.125
length/wain ratio
Obesity
Index
5
10
15
20
weeks

Growth in Physa gyrina is not determinate as it was found to be in Carychium exiguum (Harry, 1951), but continues throughout the life of the individual. During the latter period of the existence of P. gyrina, increase in size is of a pattern different from that established during early life, not only in the rate at which material is added to the shell but also in a change from longitudinal to lateral expansion.

The maximum size of the shell is primarily controlled by physiological limitations to the life span and secondarily by various environmental factors such as pollution, crowding and available food. References, in the literature, to mature snails are confusing because the meaning of the term maturity is not defined. It seems advisable to refer maturity to that point of the life-cycle at which time the snail becomes sexually mature and is capable of producing viable eggs and sperm.

Death within a field population can be attributed to a variety of causes. The species has a maximum life expectancy which depends upon its genetic constitution and the limitations of the environment. Since Physa gyrina is monoecious, a differential death rate of sexes which was a major factor in determining the composition of a population of Viviparus contectoides (VanCleave, 1934), can be disregarded. Accidental death, due to deviations from optimal ecological conditions such as pollution, and scarcity of food, did not play a significant role in the Scio population. Nearly all of the mature population died at the end of the egg-laying period in April and were replaced by juveniles.

Senility in laboratory raised snails was accompanied by morphological changes and alterations in behavior patterns. The shell became eroded and the digestive diverticula (liver) of freshly-dead specimens, had lost its normal firm texture and yellowish color and was soft and whitish in appearance. However, this change in the digestive diverticula may have been due to autolysis. As death approached, the snails became increasingly inactive. They fed sporadically (healthy snails fed more or less continuously) and remained attached to the sides of the aquarium sometimes for several days. In this inactive state, the animal was withdrawn into its shell and the foot was contracted to less than one-half of its maximum size. Eventually they lost their ability to adhere to the substrate and fell to the bottom of the aquarium where they remained, in some instances, for several days in a "paralyzed" condition before they died.

COMPARISON OF REPRODUCTION IN FIELD COLLECTED AND LABORATORY REARED *PHYSA GYRINA*

Reproduction, including copulation, oviposition, embryonic development and hatching in *Physa gyrina*, was studied during this investigation. The work consisted, in addition to the items mentioned above and discussed in detail in other sections, of two more comprehensive portions; one a study of snails collected in the field and isolated in the laboratory, the other of observations made on snails reared in the laboratory throughout their life.

Study of *Physa gyrina* Collected in the Field

The specimens studied were collected from January through April and isolated in separate containers within an hour or two after they were brought into the laboratory. They were checked daily for as long as they lived. Egg masses were removed as laid, measured, the eggs counted and the stage of development of the embryos within the eggs noted. Succeeding development of embryos within each egg mass was followed and a record of the number of embryos failing to pass through the trochophore and/or post-trochophore stages was kept. An account of the number of snails hatching from each egg mass was also made. These data are presented in Table 6.

There was no assurance that the snails taken in the field for investigation had or had not copulated. Thus it was not possible to determine whether the ova were cross- or self-fertilized but there had been ample opportunity for copulation to occur.

Table 6

Viability of Eggs Expressed in Mean Percentages

	Died as Trochophore	Died as Post-Trochophore	Hatched
	Argo Group (Laboratory Reared)		
From One Egg Mass:			
8 reared together	1	23	76
3 reared in isolation	9	27	64
From Another Egg Mass:			
3 reared in isolation	21	49	30
	Scio Group (Laboratory Reared)		
From One Egg Mass:			
2 reared together	1	42	57
From Another Egg Mass:			
6 reared in isolation	4	36	60
6 reared together in one liter water	2	7	91
6 reared together in two liters water	1	32	67
	Summary		
Collected in field and Isolated in Laboratory	7	4	89
Reared in Isolation in Laboratory	11	38	51
Reared Together in Laboratory	1	26	73

A number of these isolated snails were dissected after death to determine the extent of parasitism by larval trematodes. The obviously parasitized snails showed no difference in fecundity from those not parasitized.

The majority of the snails began to oviposit on the same day they were isolated. In one case, five days elapsed before the snail laid eggs and a total of seven masses were produced. The two smallest snails were isolated for nine and eleven days before ovipositing.

Oviposition followed the same general pattern in all the specimens studied. At first the egg masses tended to contain the maximum number of eggs and two to five egg masses were produced each day. Following this initial activity, the number of eggs generally declined. Near the end of the ovipositing period, several days might elapse between deposition of egg masses containing a relatively small number of eggs (Plate VII).

A similar decline in egg production near the end of the ovipositing period has been demonstrated in other species of pulmonate snails. In Ancylus fluviatilis (Bondesen, 1950), a decrease in egg production occurred near the end of the ovipositing period. Ferrissia fusca (= Ancylus fusca) according to Clapp (1921) also showed a marked decrease in the number of eggs per mass at the end of the ovipositing period.

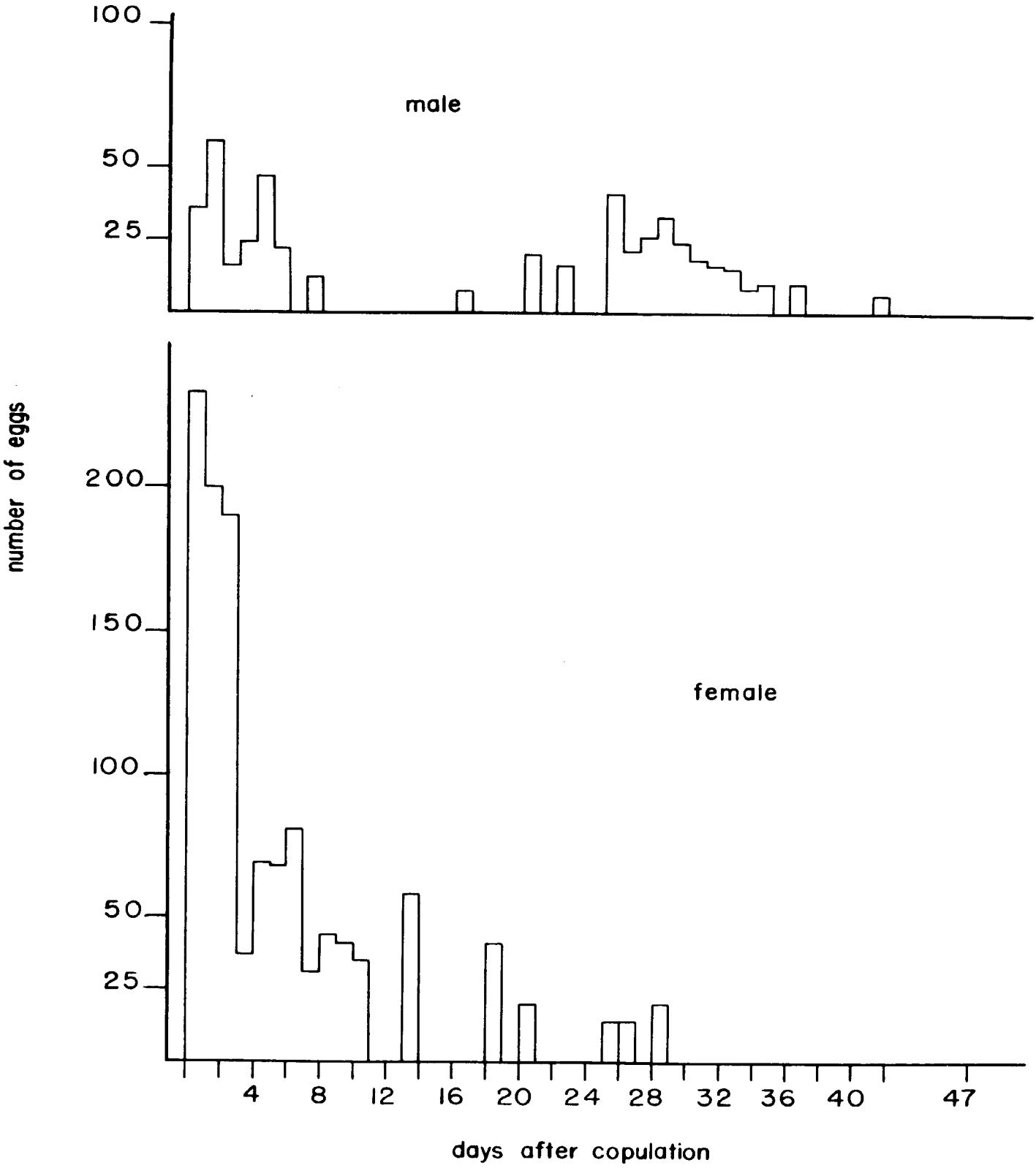
In a study of Planorbis corneus and Helisoma (= Planorbis) trivolvis, reported by Cole (1925), as egg laying continued the number of eggs per mass decreased. Gyraulus albus also



PLATE VII

Periodicity and Total Egg Production in Two Snails Isolated after Copulation. The "Female" Died 33 Days after Copulation. The "Male" Lived for 47 Days.

PLATE VII


100
50
25
male
number of eggs
200
150
100
50
25
female
4
8
12
16
20
24
28
32
36
40
47
days after copulation

showed a decrease in egg production toward the close of the egg-laying period (Bondesen, 1950).

Several species within the family Lymnaeidae have been intensively investigated. Baily (1939) demonstrated a marked decline in the production of eggs by Lymnaea columella as the ovipositing period progressed. The same general trends have been detected in L. japonica (Taki, 1931); L. luteola (Seshaiya, 1927); L. stagnalis (Noland and Carriker, 1946; Schodduyn, 1925).

No data are available in the literature pertinent to the Physidae.

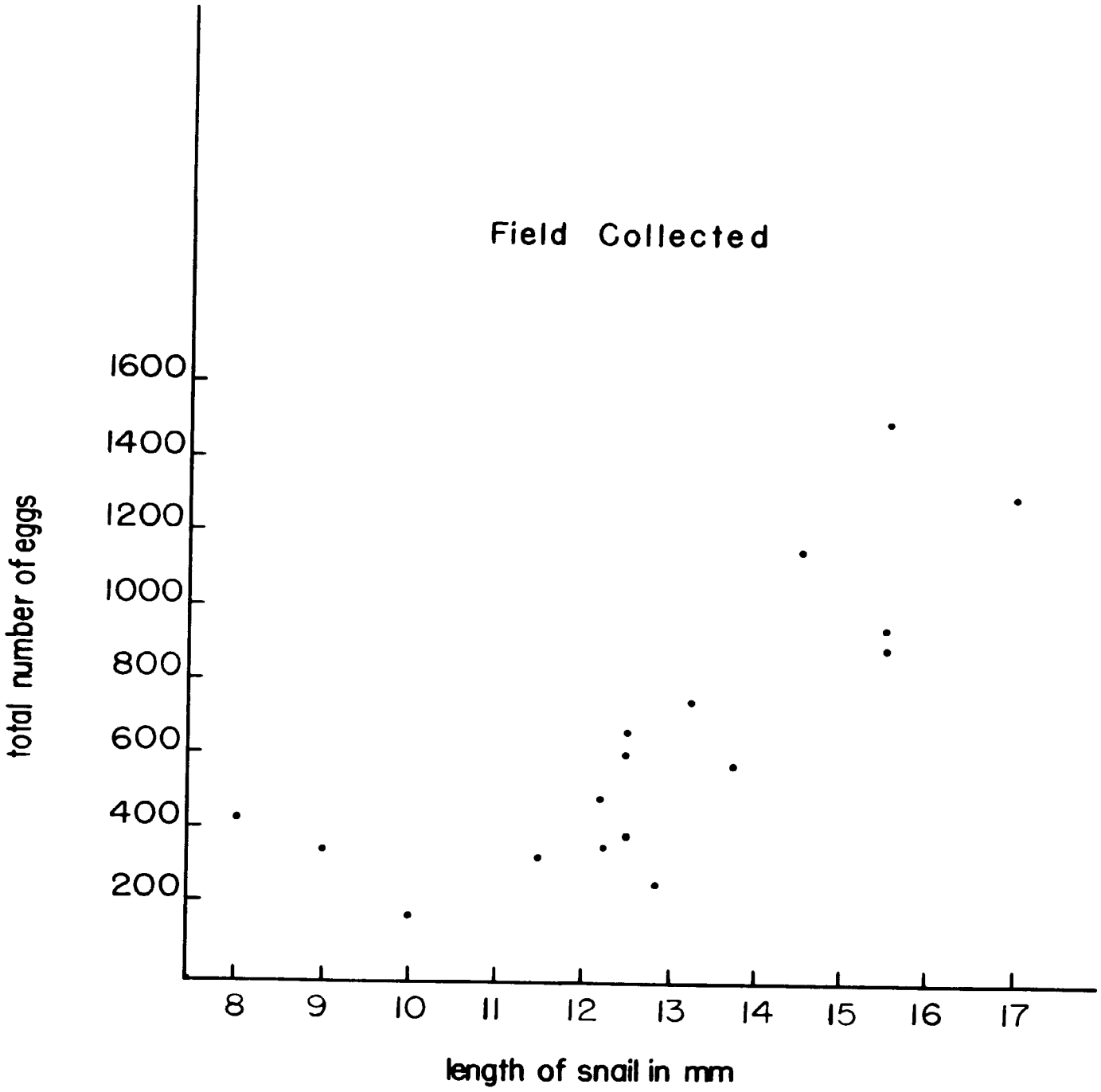
The number of eggs per mass ranged, in this study, from 2 to 118 for field collected snails that were isolated in the laboratory. The number of masses ranged from 7 to 47 per snail and the mean number of eggs per mass laid by these snails was 29 (Table 8). Compared to laboratory reared snails, embryonic mortality in the eggs from field collected individuals was low, about 11 per cent. Of those eggs which did not hatch, 7 per cent died before they had passed through the trochophore stage and 4 per cent died as post-trochophores (Table 6).

There was a definite positive correlation between the length of the snail, at the time oviposition began, and the total number of eggs produced (Plate VIII). There was no correlation of the maximum number of eggs in a single mass with the total number of eggs produced by a single snail except at the extremes of the range of total egg production. It was found that those snails laying the smallest total

PLATE VIII

Correlation Between the Length of the Snail in mm at Time of Oviposition and the Total Number of Eggs Laid. (These snails were collected in the field and isolated in the laboratory.)

PLATE VIII


Field Collected
total number of eggs
1600
1400
1200
1000
800
600
400
200
8
9
10
11
12
13
14
15
16
17
length of snail in mm

number of eggs produced masses with a minimum number of eggs while the snails laying the maximum total number of eggs deposited masses containing the greatest number of eggs.

Baker (1902; 1928) reported that Physa gyrina laid from 130 to 200 eggs per mass. His observations were made on 15 snails "kept in captivity" and which laid a total of 14 egg masses in two days. In this study 1,229 egg masses, laid by 51 snails, were examined; the number of eggs per mass ranged from 1 to 118 the mean being 21.

The number of days on which egg masses were laid was, in nearly all cases, less than the number of days over which this aspect of reproductive activity extended. As will be seen from the data presented in Table 7, the period of post-reproduction is short. These laboratory observations agree with those made on the field population.

Schodduyn (1925) isolated two individuals of Lymnaea stagnalis after they had copulated. The "female" snail started to oviposit 24 hours after pairing and laid five masses with a total of 175 eggs. The "male" individual oviposited three days after copulation and produced three masses containing a total of 47 eggs. In this study, a pair of P. gyrina were isolated after copulation. The "male" measured 12.25 mm in length, the "female" 14.5 mm. Both snails oviposited within 24 hours after pairing. The period of reproduction for the "male" extended over 42 days; during this time 26 egg masses containing 484 eggs were laid on 22 days. The reproductive period for the "female" extended over 29 days and during this time 30 egg masses containing 1148 eggs

were laid on 17 days (Plate VII). Since these two snails were part of a collection made in the field on April 19, there is no assurance that they had not copulated before (and the sex of each animal may have been reversed) nor that they had not oviposited before collected.

Study of Laboratory Raised Snails

Physa gyrina were reared in the laboratory from eggs laid by individuals collected in the field from two localities. The first site consists of a series of small pools located at the base of Argo Dam in the Huron River within the city limits of Ann Arbor. The F_1 and F_2 generations of laboratory reared snails from the stock collected there are referred to as the Argo group. The second locality at Scio is about six miles upstream from the former and is the site of the study on the field population of Physa gyrina. The laboratory raised (F_1 and F_2 generations) snails from stock obtained there are referred to as the Scio group.

Several groups of snails were selected at time of hatching from egg masses laid in the laboratory by snails collected in the field. Those reared separately were isolated at the time they hatched from the egg. There are several factors over which no control is possible in the field, but which can be controlled in the laboratory: all snails were fed the same lettuce diet throughout their life-span; the factors of light and temperature were approximately the same for all individuals; infection by larval trematodes was eliminated; the selection of all the snails within one study group from a single egg mass made the probability of their being genetically

similar much more likely; the determination as to whether Physa gyrina is self-fertile was assured.

Argo Group

Two Physa gyrina, measuring 13.50 by 7.25 mm and 13.0 by 7.75 mm, from a collection made at the Argo locality on September 23, 1951 deposited several egg masses in the laboratory the following day. Upon escape from eggs of one mass eleven snails were selected at random to be reared: a group of eight cultured together, and three which were isolated. From another egg mass three were reared in isolation. Data pertaining to the period of development, period of reproduction, the actual number of days on which egg masses were laid, the total number of masses, the total number of eggs and the period of post-reproduction are presented in Tables 7 and 8.

Scio Group

Twenty-two young Physa gyrina, hatched from egg mass 14 containing 22 eggs laid by a snail collected at Scio, were placed in an aquarium containing 16 liters of water on February 13, 1952. Twenty-one days later (March 5) two of these snails were removed and reared together in a gallon jar containing two liters of water. On March 5 all of the snails were without pigment which made it possible to observe many of the internal organs. The two snails, which had been separated from the other twenty, had acquired normal pigmentation

Table 7

Life History Data

Mean measurements are used in all categories. Time is expressed in days.

	Length in mm. at Time of Oviposition	Period Development	Period Reproduction	Number of Days on Which Egg Masses Laid	Number Egg Masses Per Snail	Number Eggs Per Snail	Period Post-Reproduction	Total Life Span
Field Collected and Isolated								
	12.8	-	25	17	22	653	4	-
Argo Group (Laboratory Reared)								
From One Egg Mass:								
8 reared together	7.0	241	76	27	5	46	184	501
3 reared in isolation	14.2	217	93	40	47	1124	112	422
From Another Egg Mass:								
3 reared in isolation	8.2	176	71	35	37	508	12	259
Scio Group (Laboratory Reared)								
From One Egg Mass:								
2 reared together	13.0	102	71	35	24	450	245	418
From Another Egg Mass:								
6 reared in isolation	12.6	114	93	40	43	859	237	444
6 reared together in 1 liter water	9.5	79	131	72	22	272	138	348
6 reared together in 2 liters water	9.0	87	98	57	20	245	203	388
Summary								
All snails reared together in laboratory	9.7	127	94	48	18	253	193	414
All snails reared in isolation in laboratory	12.0	169	86	38	42	830	120	375

17 days later. Those in the aquarium never became pigmented. On May 26, 103 days after birth, the two individuals were observed in copulo and two egg masses, laid one or two days before, were taken from the aquarium. These two snails measured 13.0 by 7.0 mm and 12.75 by 6.75 mm at this time. (The parent snail measured 12.5 by 7.0 mm at the time it began oviposition.) The 20 snails in the large aquarium did not deposit eggs until 118 days after birth. The vital data pertaining to the two raised together are presented in Table 7.

A second group of snails, obtained from an egg mass containing 33 eggs laid by another snail on January 25, 1952 and hatched seven days later (February 1), were studied. The parent snail measured 12.50 by 7.0 mm at the time of oviposition. Six snails from this egg mass were isolated at birth and measurements taken at regular intervals to determine the rate and nature of growth (Table 5). Vital data concerning these six snails are summarized in Tables 7 and 8.

Twelve other snails hatching from the same egg mass laid by the same snail as above were selected at random and divided into two groups of 6 each. The first group was reared in one liter of water, the second in two liters. Data pertaining to these groups of snails are presented in Tables 7 and 8.

The F_1 generation of Physa gyrina, from both the Argo and Scio stocks, reared in isolation proved to be self-fertile. That parthenogenetic development of ova, produced by isolated snails, did not occur was demonstrated by the formation of

two polar bodies during maturation of the ova.

Self-fertilization among monoecious metazoa, both free-living and parasitic, is rather common. Gavrilov (1935) has summarized the literature for all groups but rather sketchily in the case of the pulmonate snails. Larambergue (1938) has an excellent resume for both the basommatophoran and stylommatophoran snails. Within the former suborder, thirteen species of the family Lymnaeidae, eight of the Planorbidae, two of the Bulinidae and one of the Ancylidae are reported to be self-fertile. Twenty species included in five families of Stylommatophora are reported in which self-fertilization occurs.

The ability to self-fertilize is not possessed in the same degree by all families of pulmonate snails. It appears to be exceptional in the Helicidae, Ancylidae and certain of the Planorbidae. However, in the Lymnaeidae, Colton (1922) reared L. columella for forty-seven generations in isolation and Holzfuss (1914) reared L. stagnalis four generations in isolation.

Six species of Physa are reported to be capable of producing viable eggs without copulation. There are no reports, however, of any species of Physa in which the isolated F_2 generation produced eggs which hatched. Viable eggs from isolated individuals of Physa acuta were obtained by Holzfuss (1914) and Larambergue (1938). Crabb (1927) isolated individuals of Physa gyrina and P. sayii and obtained "viable" eggs but he did not state whether or not these eggs hatched. P. heterostropha, according to Colton (1918), produces fertile

eggs when reared in isolation but again there is no statement as to whether or not snails hatched from such eggs. In some of the instances cited above, the criterion of self-fertility appears to have been that the isolated snail grew to maturity and laid eggs which in their turn "developed."

From the results of this study on Physa gyrina it is obvious that although eggs of "virgin" snails may undergo development, even as far as the stage in which a shell is fully formed, the critical factor in determining whether a species can reproduce by self-fertilization for several generations is that the progeny of "virgin" snails must hatch, develop and produce eggs which in their turn develop and hatch to form another generation.

Only one individual of the F_2 generation of Physa gyrina raised in isolation or together, in this investigation, laid eggs which hatched to produce the F_3 generation. Individuals of the F_2 generation from both Argo and Scio stocks were reared together and in isolation. Four snails hatched from the first egg mass laid by an F_1 individual from Argo stock were reared together in two liters of water. On June 8 (72 days after birth) three egg masses with a total of 21 eggs were laid. Five more masses containing 43 eggs were found on June 20 and three days later another mass of five eggs was laid. The last mass of two eggs was deposited June 30. All of the ova failed to gastrulate - death occurred during late cleavage in most cases.

A single individual from the same parent and egg mass as the preceding four snails was reared in isolation. Seventy

days after birth, this snail laid 16 egg masses with a total of 74 eggs within one week. None of these ova developed beyond early cleavage, death occurred either before or shortly after the first division had taken place. This snail died at the age of 114 days.

Two additional snails of the same parentage were reared in isolation. Neither oviposited; one died at the age of 115 days, the other lived for 127 days.

Five snails of the F_2 generation hatched from the first egg mass laid by another snail (F_1 of Argo stock) were isolated at birth. Fourteen days later four were dead. The fifth lived for 145 days but laid no egg masses during that time.

Another F_2 individual from Scio stock lived 148 days without ovipositing while one from Argo stock lived 340 days and laid no eggs.

The one isolated snail (of the F_2 generation) which laid eggs that hatched came from Scio stock. Oviposition began when it was 220 days old and up to this date 152 eggs have been laid and 44 per cent have hatched.

DISCUSSION

The ecological ages of a field population of Physa gyrina are, with a few exceptions, rather different from the ages of laboratory raised snails. Field observations made on P. gyrina generally agree with those made on other animals (Allee et al., 1949) in that the period of post-reproduction is shortest and the period of development is longest. This is undoubtedly due to unfavorable winter conditions. The same relationships do not hold true in laboratory reared specimens. Here the period of reproduction is generally the shortest and the period of post-reproduction, on the average, far exceeds that of snails in the field. This is due perhaps, to laboratory conditions that are optimal for the existence of the snail such as freedom from parasitism.

The average length of life in laboratory reared individuals was greater than in snails living in their natural habitat. There they live for 12 to 13 months, while in the laboratory the life span of some individuals extended over 19 months (Table 7). Crabb (1929) indicates that Lymnaea stagnalis apressa lives for a shorter period of time in the laboratory than in the field and attributes this to a lack of rest-periods which occur seasonally in nature. Thus he postulates that the snail's life in the laboratory was shortened by a continuous relatively high metabolic activity. One factor which shortens the life of laboratory raised Physa gyrina is high egg production. The length of life of snails reared in isolation and those reared together was not appreciably different in the

Scio group. Those reared in mass culture from the Argo locality lived much longer than isolated individuals.

It is difficult to account for the disparity between snails from Argo and Scio reared under identical laboratory conditions. The data are presented in Tables 6 and 7. The Argo group, although derived from parents as large and apparently as vigorous as those from Scio, tended to have a longer period of development, a shorter post-reproductive period and thus a shorter life span than the Scio group. However, within the Argo group, two series of isolated snails derived from two different egg masses and possibly different parents were quite unlike. The mean length of shell at time of oviposition, average number of eggs laid per snail, and the average life span were greater in the first series than in the second. These variations between and within the two groups indicate physiological differences in Physa gyrina such as were found by Baily (1939) in Lymnaea columella.

The seasonal periodicity of oviposition in Physa gyrina, which exists under field conditions, tends to disappear in the laboratory. The egg laying period begins when the snails have reached a certain morphological and physiological state of development, regardless of the season.

The observations of Boycott et al (1930) and Noland and Carriker (1946) that snails raised in isolation begin ovipositing much later than do those reared together do not apply in the case of Physa gyrina. Again, a dissimilarity was found between the Argo and Scio groups. Communally raised snails of the former group laid eggs later than any of those in isolation

while in the Scio group the opposite was true (Table 7).

The study on oviposition and percentage of hatching in field collected and laboratory reared Physa gyrina are summarized in Table 6. The most striking feature of this aspect of the study is the large number of eggs produced by isolated snails and the decrease in egg production per individual as the number of snails raised together is increased. The data concerning snails collected in the field and isolated in the laboratory may not be a true representation as some of those individuals may have oviposited before collection. The data for laboratory reared specimens is complete as they were under observation from birth to death.

Crabb (1927) stated that pond snails isolated "in ovo" laid as many eggs as those individuals reared in mass cultures. This is not true of Physa gyrina, a "typical pond snail." Isolated individuals laid twice as many eggs as two individuals reared together; three times as many as six individuals and eighteen times as many as eight. This high egg production in isolated Physa gyrina may be a compensatory factor because, contrary to Crabb's (1927) report, the percentage of hatching in these "virgin" eggs is considerably lower than in those snails in which cross-fertilization can take place. In view of these findings and the fact that only one of the individuals of the F_2 generation, raised in isolation or together, produced eggs which hatched it is impossible to accept Crabb's statement (1927) that "self-fertilization is the normal method of reproduction in pond snails."

An aspect of this study, which may be of value in the

Table 8

Comparison of Reproduction in Snails from a Natural Population and Snails Reared in the Laboratory

	17 Snails Collected in Field and Isolated in Laboratory	Laboratory Reared Snails			
		12 Reared in Isolation	Together		
			2	6	8
Mean Number of Egg Masses per Snail	22 (7 - 47)	42 (4 - 73)	24	21	5
Mean Number of Eggs Per Mass	29 (6 - 118)	20 (1 - 86)	19	12	9
Mean Number of Eggs Per Snail	653 (159 - 1500)	838 (42 - 1841)	450	259	46
Percentage of Eggs Hatched	89 (44 - 100)	51 (22 - 93)	57	79	76

The numbers in parentheses are the ranges for each category.

laboratory culture of Physa gyrina, when space is limited, is the large variation in the number of progeny that can be obtained when different numbers of individuals are raised together. From the data obtained in this study (Table 8), optimum conditions can be ascertained by multiplying the mean number of eggs per snail by the percentage of eggs which hatched by the number of snails per culture. This calculation will give the number of young snails produced under varying conditions. The results are presented below.

Table 9

Total Number of Offspring Obtained Under Varying Conditions

Field Collected and Isolated	Reared in Isolation	Reared Together			
		2	6*	6**	8
581	427	513	1469	985	280

* in one liter of water

**in two liters of water

The results obtained from the experimental conditions set up in this investigation indicate that, as far as significant reproductive capacity (the actual numbers of normal progeny obtained) is concerned, optimal conditions appear to have been met when six snails were reared together in one liter of water. Furthermore, this group of six snails (from the same egg mass as the group of six reared in two liters of water) was larger (mean length of shell) at the time of oviposition, laid a greater number of eggs per snail and had 24

per cent more of its eggs hatch than the group in two liters of water. Allee has demonstrated that goldfish grow better in water in which similar goldfish have lived than they do in water changed daily. He states that this is due to a partial distribution of available food and the liberation (by the fish) of a growth-promoting substance into the environment (Allee et al, 1949).

A demonstrable difference in length of shell at time of oviposition exists between isolated and mass cultured snails. Smaller snails resulted when crowding was increased and there was a decrease in egg production which varied directly with decrease in size (Table 10). A positive correlation also exists between length of shell and total number of eggs produced by individuals collected in the field (Plate VIII). Snails raised in isolation also exhibit the same direct relationship between shell length and individual egg production as do those in mass cultures (Table 11).

Table 10

Correlation Between Size and Egg Production in Snails Reared in Mass Culture

	Mean Length of Shell in mm. at oviposition	Mean Number of Eggs Per Snail
8 snails (1-1) from Argo	7.0	46
6 snails (9EM6-8) from Scio	9.0	245
6 snails (9EM6-7) from Scio	9.5	272
2 snails (8EM14) from Scio	13.0	450

Table 11

Correlation Between Size and Egg Production in Snails Reared in Isolation

	Mean Length of Shell in mm. at oviposition	Mean Number of Eggs Per Snail
3 snails (2-3, 2-4 and 2-6) from Argo	8.2	64
6 snails (9EM6-1 through 9EM6-6) from Scio*	12.6	859
3 snails (1-2, 1-3 and 1-4) from Argo**	14.2	1124

* From the same egg mass as 9EM6-7 and 9EM6-8

** From the same egg mass as 1-1

That Physa gyrina can maintain itself through self-fertilization for one generation has been experimentally established in the laboratory. The general failure to produce an F_3 generation, under experimental conditions, may be due to factors in the laboratory that are not conducive to the reproduction of this generation. However, this does not appear to be the case since the F_2 generation was reared under the same conditions so successfully used for the F_1 generation. That it was due to some genetic combination within a single population seems unlikely because, with the exception of one snail, F_2 individuals from both the Argo and Scio stocks did not produce eggs which hatched. As has been stated before, the families of pulmonate snails possess the capability for self-fertilization in varying degrees.

In their natural habitat, individual Physa gyrina may become isolated from other members of the population or an individual may be transported in some manner to a new and favorable environment uninhabited by any members of its species. Ability to reproduce through self-fertilization, even for a single generation, would be of unquestionable value in the maintenance and dissemination of the species.

SUMMARY

1. Temperature is the initiating and controlling factor in oviposition by sexually mature Physa gyrina. The range which appears to be optimal is from ten to twelve degrees Centigrade.
2. Physa gyrina is a typical inhabitant of temporary and semi-permanent bodies of water. In temporary ponds, it survives periods of dryness by estivating in bottom materials.
3. The life cycle of P. gyrina living in a semi-permanent habitat (Scio) was investigated.
    A. Eggs are laid by adults in April.
    B. The adult population dies after oviposition and is replaced by juveniles.
    C. Some individuals hatching in the spring may become sexually mature in the fall of the same year, but due to low temperatures, most oviposition is delayed until the following spring.
    D. The life span of individuals in the field is from twelve to thirteen months.
4. The life cycle of P. gyrina in a pond (Black River), 300 miles north of the habitat near Ann Arbor, was essentially the same with the exception of a delay in reproductive activity due to lower mean monthly temperatures.
5. The life cycle in a temporary pond (Kenk Pond II) is complicated by a period of summer dryness during which metabolic activities cease.

A. Individuals born in the spring in such situations rarely attain sexual maturity by the following fall.

B. Depending upon the extent of the dry period, the time needed to reach sexual maturity is varied.

6. The development of the embryo, at room temperatures, was observed at daily intervals.

A. The features characterizing the various stages are described.

B. On the fourth day following oviposition, the embryonic snail had assumed the external appearance of the adult.

C. Hatching occurred on the seventh day.

D. That embryonic development is directly related to temperature was demonstrated by comparing development in two egg masses, one kept at room temperature, and the other at four to five degrees Centigrade.

7. The rate of embryonic growth was determined by measuring increase in the diameter of developing snails kept at room temperature. Average geometric growth rates were calculated.

8. Post-embryonic growth rates, as determined by length-width measurements of the shell, were studied in a group of isolated snails hatched from the same egg mass. Additive growth rates were calculated.

A. The shell grew faster along the longitudinal than along the lateral axis, during the first fourteen

weeks of life.

B. Lateral expansion of the shell characterized the growth during the remainder of the life span.

9. The presence of "rest marks" on the shell was concluded not to be dependent upon environmental factors but rather a result of a physiological pattern developed within the species.

10. Growth in P. gyrina is not determinate but continues throughout the life of the individual.

11. Senility was accompanied by morphological changes in the shell and by alterations in behavior patterns.

12. Experimental work on reproduction was conducted on snails collected in the field and on those reared in isolation and together in the laboratory.

13. There was a decline in egg production near the end of the ovipositing period.

14. A definite positive correlation existed between the length of the snail, at the time oviposition began, and the total number of eggs produced in both field-collected and laboratory-reared individuals.

15. The number of days on which egg masses were laid was less than the total number of days over which this particular aspect of reproduction extended.

16. Two snails were isolated after copulation. The "female" laid a larger number of eggs and lived for a shorter period of time than the "male."

17. The ecological ages of a field population are not the same as those ages of laboratory reared snails. In the field,

the period of development is longest and the period of post-reproduction shortest. In the laboratory, the period of reproduction is shortest and the post-reproductive period far exceeds that of a field population.

18. The average length of life of laboratory raised snails exceeded that of snails living in their natural habitat.
19. A high egg production appreciably shortens the life of laboratory reared individuals.
20. Diversity in size, egg production, embryonic mortality and total life span, within and between groups of P. gyrina from different localities, indicates the existence of a physiological group differentiation within the species.
21. Seasonal periodicity of oviposition in P. gyrina, which exists under field conditions, tends to disappear in laboratory reared snails.
22. P. gyrina reared in isolation do not begin to oviposit appreciably later than do those reared together.
23. In laboratory raised P. gyrina, isolated individuals lay a much larger number of eggs than do those reared together.
24. Egg production per individual decreases as the number of snails reared together is increased.
25. An inverse proportion exists between the length of the snail and the number of snails reared together.
26. The percentage of hatching in "virgin" eggs is considerably lower than in those eggs produced by snails in which cross-fertilization can take place.

27. Optimal conditions for obtaining the largest number of progeny in limited laboratory space appear to have been met when six snails were reared together in one liter of water.

28. Physa gyrina can successfully reproduce through self-fertilization for one generation in the laboratory. The second generation, reared in isolation, exhibited a great decrease in production of viable eggs.

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