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LIFE HISTORY AND GROWTH OF THE SNAIL
LYMNAEA HUMILIS SAY

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By

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LIFE HISTORY AND GROWTH OF THE SNAIL, *LYMNAEA HUMILIS* SAY¹

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INTRODUCTION

Lymnaea humilis Say is an amphibious pulmonate snail which is able to live in a variety of habitats; however, it generally occurs in fewer numbers in water than on land, and attains its peak abundance on mud flats (McCraw, 1959). In his extensive study of the Lymnaeidae, Hubendick (1951) has discussed the systematic position of *Lymnaea humilis* Say. In the present investigation, life history studies were carried out at two localities on the Raisin River, southwest of Ann Arbor, Michigan. One of these was located three miles southwest of Clinton, at Newburg, in Lenawee County; the other was located about one mile northwest of Clinton in Washtenaw County. The two stations are designated as the Newburg and Clinton habitats, respectively.

METHODS AND MATERIALS

At Newburg, quantitative samples were gathered according to a method already described (McCraw, *l.c.*). During the winter months when the snail population in this area became low, quantitative samples were supplemented with leaf samples, or an area was scraped extensively with a spatula. This assured a sufficiently large sample for a seasonal population analysis. The Clinton area was not sampled quantitatively but sufficient snails were collected for an adequate population study, using a spatula, or by harvesting leaf material. In the laboratory this type of sample was placed in shallow enamel pans. *L. humilis* were removed by hand-picking after they came to the surface of the water or crawled along the edges of the pan. Leaf and other materials were also examined for live snails. The material in the pans was observed for about a week to assure removal of all living snails. The water was then drained or siphoned carefully from the pans and leaves or bottom deposit allowed to dry. A further examination was then made for dead snails which were kept separate from the living ones. During the winter, monthly collections were made from these two localities whereas from May 15 to August 21, 1954 samples were taken approximately every two weeks.

Snails required for laboratory rearing were measured immediately and kept alive in suitable containers. The remainder were relaxed with menthol, fixed and preserved, or preserved unrelaxed. These snails were measured at a later time. In studying the natural population only the maximum length of the shell was taken. The maximum length and the greatest width perpendicular to the length were measured for snails reared in the laboratory, or those used in the growth analysis of a natural population. The length and width of the aperture as well as measurements of certain anatomical structures were also taken. For this, a dissecting

¹Contribution from the Department of Anatomy, Ontario Veterinary College, Guelph, Canada, and from the Museum of Zoology, University of Michigan, Ann Arbor. Part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, University of Michigan.

microscope with a calibrated ocular micrometer was used. Shell dimensions were determined with the aperture of the snail facing the observer and the axis of the snail parallel to the stage of the microscope.

LIFE CYCLE AND SEASONAL DISTRIBUTION

The Newburg and Clinton localities were first visited in September, 1953. At this time, in each of these areas recently hatched snails were present (Fig. 1 and 2). Measurements of a number of snails hatched in the laboratory showed that when they emerged from the egg mass they averaged 0.68 mm. in length and 0.54 mm. in width. Thus, in each of these habitats many of the juveniles had hatched within one week of collecting and a large number at Newburg had undoubtedly hatched that day. In spite of the large number of young, egg masses were not common. From this time to the onset of winter conditions, the increase in size of *L. humilis* from month to month gradually became less. This is indicated by the smaller shifts in the distribution of size classes (Figs. 1 and 2). In each habitat growth was inhibited to the level of the winter minimum by the latter half of November; however, ovipositing continued until about the middle of November. Little growth occurred from the months of December to March when both air and water temperature were below ten degrees C. During February and March very few snails were found. This scarcity was due to heavy rains during the middle of February which raised the water level resulting in snails being swept away along the banks of the river and from the mud flat.

In spring, initiation of more rapid growth and ovipositing is controlled by temperature. DeWitt (1955) has shown that copulation and oviposition in *Physa gyrina* Say does not take place until the water temperature has reached ten to 12 degrees C. Field observations indicate that this is also true for *L. humilis*. In April when the water and air temperatures were 13 and 20 degrees C. respectively, large numbers of egg masses were seen. *L. humilis* evidently oviposits both in and out of water as egg masses were present approximately 50 cm. either side of the land-water junction upstream from the flat at Newburg. At the Clinton locality, they were also present on the river bank and under water, a few centimeters in both directions from the water's edge. They were always seen in greatest numbers, however, on land along a narrow region adjacent to the shoreline. The width of this region decreased with an increase of the slope of the ground.

Observations of snails in the laboratory showed that *L. humilis* did not oviposit if they were less than four mm. in length. Size of the snail is a better index of sexual maturity than age because rate of growth is largely governed by temperature. DeWitt (*l.c.*) has shown that length is the most reliable index of sexual maturity in *P. gyrina*, and he found that neither field collected nor laboratory-raised snails oviposited before reaching seven mm. *Lymnaea truncatula* Müller, which attains a maximum size about equal to *L. humilis*, oviposits after reaching an altitude of four to 4.5 mm. (Walton and Jones, 1926).

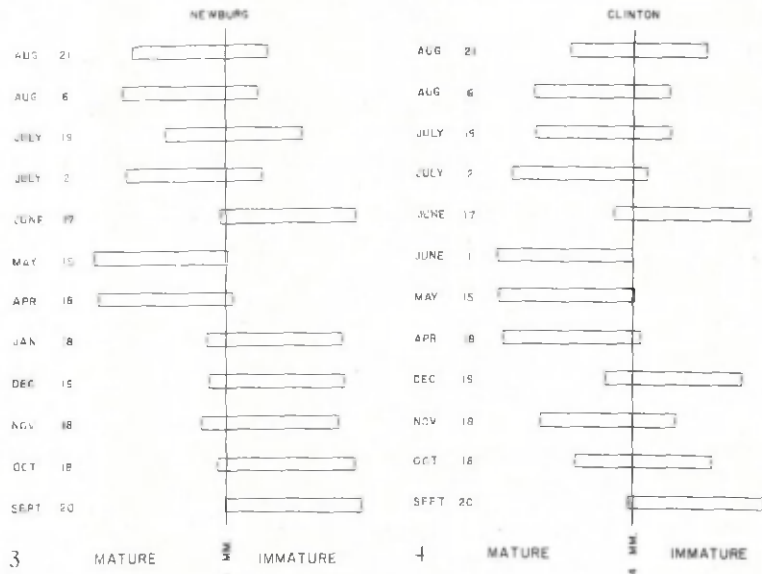
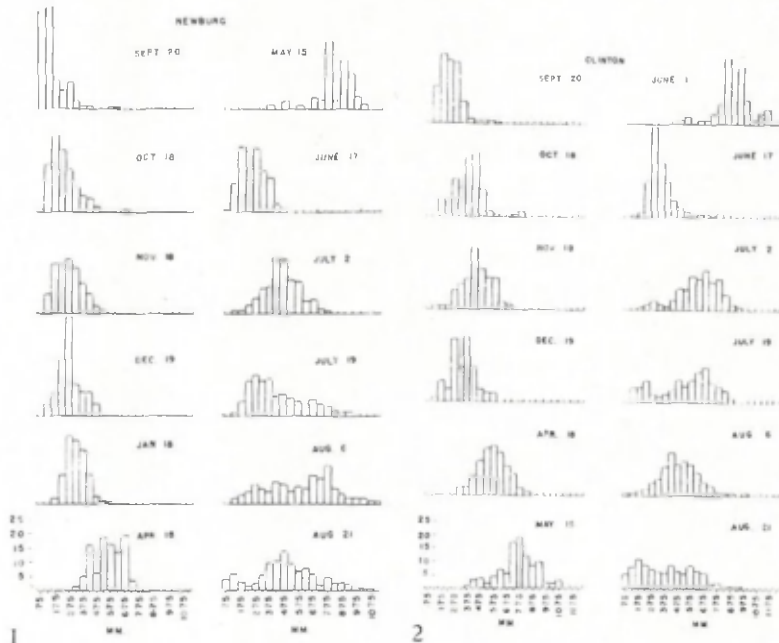
In April about 95 percent of *L. humilis* were sexually mature (Figs. 3, 4). Most of them were recently matured and they laid a large quantity of egg masses at that time. Ovipositing by these snails which have overwintered continued until the end of May or early June. At this time these snails die. Collections at Clinton on June 1st showed that the

population consisted mostly of large, and consequently aged snails (Fig. 2). This population represents those snails which have over-wintered. Within the next two weeks this age group died. On the other hand, at Newburg none of the larger snails which had over-wintered could be found by June 1st, but they were present on May 15th (Fig. 1). Thus, there are slight variations in the length of life of *L. humilis* from habitat to habitat. It is remarkable how quickly over-wintering snails disappear when they die in late spring. Those dying under water are soon swept away or buried in deposits but even the snails that die on land disappear in a few days. In winter dead shells tend to accumulate on land, especially in December and January. Undoubtedly many of the animal remains are eaten, and the shells may be destroyed in the process. It is also probable that acids from the disintegration of the animal portion of *L. humilis* act upon the shell aiding in its destruction. The maximum size attained by *L. humilis* in late spring was just under 12.5 mm. in length. Shells over ten mm., however, were not common but those just under this size could be easily obtained (Fig. 1 and 2). *L. truncatula* reaches a maximum altitude of ten mm. (Walton and Jones, 1926). The largest shell of *Fossaria modicella* (= *Lymnaea humilis*) (Hubendick, l.c.) found by Van Cleave (1935) was 8.6 mm. in length.

Although no young *L. humilis* were present on June 1st at either Newburg or Clinton, frequency distributions for the middle of June showed that a good average size at this time was 2.75 mm. in height (Figs. 1, 2). Many of the new generation had even exceeded this size at the end of the 17-day period beginning June 1st. In order to assure that no recently hatched snails were being overlooked, the surface of the mud was carefully gone over with a spatula on both the June collecting days. By July 2nd the mode of the size distribution at Clinton had shifted to 6.75 mm. At Newburg growth of the new generation was slower; most snails were clustered about a mode of 4.5 mm. at this time. From July 2nd on, it was impossible to detect distinct modes. DeWitt (l.c.) found that early growth of *P. gyrina* was so rapid that age differences between broods laid by a single parent may be prominent, and the effect of differential growth rates, together with localized environmental inhibi-

EXPLANATION OF FIGURES

- FIG. 1. Collections of *Lymnaea humilis* from the Raisin River, Newburg, Michigan, plotted according to the percent of individuals falling within certain size classes. Numbers collected on February 18, March 19, and June 1 were too small to warrant plotting.
- FIG. 2. Collections of *Lymnaea humilis* from the Raisin River, one mile north of Clinton, Michigan, plotted according to the percent of individuals falling within certain size classes. Numbers collected on January 18, February 18, and March 19 were too small to warrant plotting.
- FIG. 3. Percent of sexually immature and mature *Lymnaea humilis* collected on the Raisin River at Newburg throughout a twelve-month period. Numbers collected at Newburg on February 18, March 19, and June 1 were too small to warrant plotting. A shell length of four mm. was found to be the size below which snails are sexually immature.
- FIG. 4. Percent of sexually immature and mature *Lymnaea humilis* collected on the Raisin River one mile north of Clinton throughout a twelve-month period. Numbers collected at the Clinton locality on January 18, February 18, and March 19 were too small to warrant plotting. A shell length of four mm. was found to be the size below which snails are sexually immature.



tors and stimuli, contributed to the heterogeneity within a population of this snail. As soon as *L. humilis* become sexually mature in summer they oviposit and ovipositing continues throughout the summer and fall months until a decrease in temperature inhibits this function.

Copulating *L. humilis* were not observed in the field. Sections of the seminal receptacle of a number of snails did not show spermatozoa, only varying amounts of cellular debris. Copulation must occasionally occur, however, as it has been seen in the laboratory. Colton (1918) reported seeing *Lymnaea humilis modicella* (= *Lymnaea humilis* (Hubendick *l.c.*) in copulation. The related *L. truncatula* evidently does not copulate either in the field or in the laboratory (Walton, 1918). Self-fertilization in *L. humilis* is probably the normal method of reproduction. Crabb (1927a, b, c) believed this method was the usual one for *Lymnaea stagnalis appressa* Say and histological studies by this author (Crabb, 1928) showed that self-fertilization occurred in *Lymnaea palustris* Müller.

The egg masses of *L. humilis* are transparent. They vary in shape from ovoid, to reniform and curved-elongate. The shape depends upon the number of eggs present; when only two or three occur the egg mass is ovoid. The general structure of an egg mass of *L. humilis* agrees with that of *P. gyrina* (DeWitt, 1954). If deposited on mud the masses are usually covered with silt which makes them difficult to detect. Under water they are more free of deposit. The egg masses are usually not over five mm. in the largest dimension. The average number of eggs per mass was ten with 16 or 17 sometimes occurring. In the laboratory they hatched between nine and 14 days after oviposition; the average time was ten days. *L. truncatula* averages seven to nine eggs per mass (Walton, 1918) and the time that elapses between oviposition and hatching is 20 to 21 days; the range is 12 to 26 days (Walton and Jones, 1926). Bondesen (1950) recorded up to 15 eggs per mass for *L. truncatula*. In nature the egg masses of *L. humilis* are subjected to a greater variation in temperature than those of typical aquatic snails. This fluctuation is because many are laid on mud and those deposited in water are near shore where it is shallow, often only one or two cm. deep, and changes in water temperature are consequently great. Diurnal variations in temperature as well as changes from day to day undoubtedly result in numerous adjustments in the rate of growth of both unhatched and hatched snails. Diurnal changes in temperature on the mud flat habitat are especially great in the spring and fall seasons.

The mechanics of hatching of a pulmonate snail (*P. gyrina*) have been accurately described by DeWitt (1954). Observations in the laboratory on hatching snails showed that *L. humilis* had difficulty escaping from the external membrane if egg masses were subjected to drying for three or four days. Evidently the external membrane becomes tough after drying and it has a tendency to remain so even after the egg mass is moistened again. Walton (1918) found that drying of egg masses of *L. truncatula* caused a prolongation of hatching time after return to moisture. Toughening of the external membrane may have accounted for part of this prolongation. Walton (*l.c.*) found that the closer to hatching time the more susceptible *L. truncatula* were to drying; no snails hatched from egg masses experimentally dried just prior to hatching.

After hatching, growth of *L. humilis* in the field is rapid. As mentioned previously, it is possible to follow shifts in the modes of population samples

for about one month after the first spring batch of egg masses has hatched. It was estimated that in June *L. humilis* increased its shell length at the rate of seven percent per day in the Clinton locality. At this rate sexual maturity is reached in about 22 days. Vaughn (1953) found that growth occurred in young *L. stagnalis appressa* at constant temperatures between 11.0 and 28.2 degrees C. with the least mortality in the 15.7 and 20.1 degree C. groups. Snails kept at 32.0 and 36.0 degrees C. died in a week. In the summer months mud flat temperatures often went above 28 degrees C. during the day and even water temperatures of 25 degrees C. and over were not uncommon. High temperatures are unlikely to be a problem for *L. humilis* on land because oxygen concentration is not critical.

Boycott (1936) stated that the greatest mortality among snails occurred in the young. Both adult and egg mortality he believed, were relatively low. He estimated that perhaps one in 500 *Lymnaea peregra* Müller young survive. Juvenile mortality of *L. humilis* was high in the laboratory and it is probable that this is true in the field but an estimate of the death rate is extremely difficult. Young snails one to three cm. in length are delicate and easily crushed or swept away and these factors are probably most important in juvenile mortality. The susceptibility of young to desiccation has already been discussed (McCraw, 1959).

The concentration of *L. humilis* on a mud flat varied seasonally. It was highest in late summer and early autumn when concentrations of over 220 snails per sq. dm. may be present (Figs. 5, 6). During the spring and summer months the reproduction rate was high and the number of snails gradually built up to a maximum. As cooler weather set in, the number of young produced gradually decreased. Coincident with the seasonal reduction in air and water temperatures, there was a corresponding decrease in the concentration of living *L. humilis*. By the middle of January it was found to be below 50 per sq. dm. (Fig. 6). The onset of lower temperatures also resulted in a rise in the number of deaths. Very few dead snails were seen in the November collecting days but 30 percent of snails collected in December were dead. In January about 20 percent of *L. humilis* taken were dead. No accurate determination of the death rate was possible as the shells of dead animals not only tend to accumulate during the winter months but it is impossible to account for those that are washed away as a result of periodic rains or wet snowfalls. These conditions make it difficult to determine the number of deaths in a given time. Field observations suggest, however, that the number dying is initially high and gradually tapers. The majority dying at this time were four to five mm. in length. At Newburg the mode of population samples for November, December and January was 2.75 mm. This figure suggests that the smaller *L. humilis* are able to survive the change from autumn to winter conditions better than larger forms. Van Cleave (1935) found that the adverse conditions of winter materially reduced the population of *Fossaria modicella* (= *Lymnaea humilis*) (Hubendick, l.c.). With the onset of winter he noticed a marked decrease in the number of large snails and he believed this reduction was due to retardation of growth rate rather than the elimination of snails that had attained a large size.

Heavy rains in the middle of February brought about a sharp rise in the water level of the Raisin River resulting in the complete immersion of the mud flat at Newburg. Fast currents and consequent heavy deposits

resulted in the dispersal of the remaining snails on the flat. No snails were found just after the rains in February. Two *L. humilis* were collected from the submerged flat in March but none were taken in April. By May the flat had reappeared but the concentration remained below two snails per sq. dm. until August 6th when a maximum concentration of eight per sq. dm. was recorded (Fig. 6). Two weeks later (August 21st) the maximum concentration and distribution of *L. humilis* reached similar proportions to those of the previous summer and autumn. Thus the study of the recovery of a population of *L. humilis*, that has been reduced to a minimal level, shows that the increase in numbers is slow at first but rapid in the final stages.

The distribution of *L. humilis* in water did not vary appreciably throughout the year (McCraw, 1959). The concentration was always much lower than on land, and, except for a few centimeters from shore it was generally below 16 per sq. dm. There was also no evidence that *L. humilis* made any attempt to burrow in mud. This is true of *L. truncatula* when subjected to natural or artificial drying (Walton, 1918).

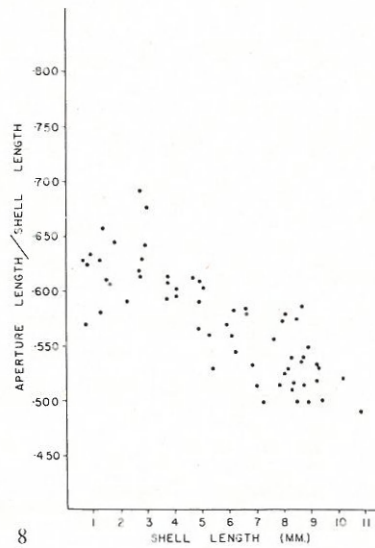
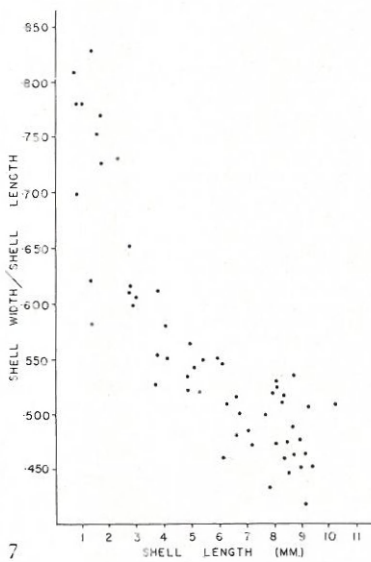
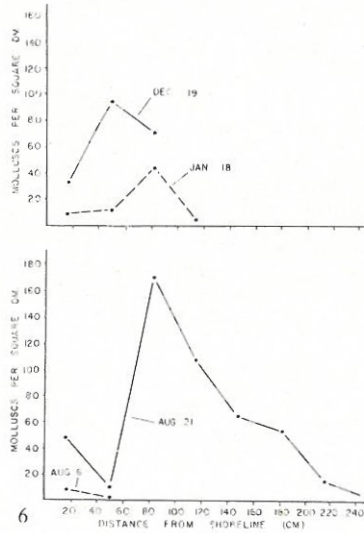
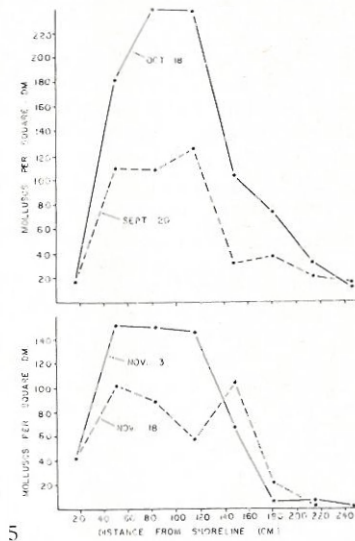
GROWTH

While studying the gross anatomy of *L. humilis* (McCraw, 1957) it was evident that the relative dimensions of some features of the shell obviously varied in relation to shell-length. This variation was apparent because young snails were more stout, and older ones more elongate in shape. Shells of *L. humilis* from the habitats studied were evenly contoured; however, the outer surface of the shell of *L. humilis* was generally covered with elongate, shallow depressions.

Width-length ratios of the shell change in relation to shell-length in a population of *L. humilis*. In general, there is a pronounced decrease in this ratio with an increase in shell-length of snails from the habitats studied (Fig. 7). The rate of elongation is greatest in shells up to about four mm. in length. Considerable variation is evident in the width-

EXPLANATION OF FIGURES

- FIG. 5. The seasonal distribution of *Lymnaea humilis* on a mud flat. The maximum concentration, expressed in molluscs per sq. dm., is attained in late summer and early autumn and then gradually decreases during the winter months. From midwinter (February 18) until early May the flat was obliterated owing to seasonally high water. By May 15 the water level had dropped and the mud flat reappeared, but the maximum concentration of *L. humilis* remained less than 3 per sq. dm. until August 6. By August 21 the maximum concentration had reached a level similar to that of the previous autumn.
- FIG. 6. The seasonal distribution of *Lymnaea humilis* on a mud flat. The maximum concentration, expressed in molluscs per sq. dm., is attained in late summer and early autumn and then gradually decreases during the winter months. From midwinter (February 18) until early May the flat was obliterated owing to seasonally high water. By May 15 the water level had dropped and the mud flat reappeared, but the maximum concentration of *L. humilis* remained less than 3 per sq. dm. until August 6. By August 21 the maximum concentration had reached a level similar to that of the previous autumn.
- FIG. 7. The relation between the ratio, shell-width/shell-length, and shell-length in a population of *Lymnaea humilis*.
- FIG. 8. The relation between the ratio, aperture-length/shell-length, and shell-length in a population of *Lymnaea humilis*.



length ratios of shells of similar length (Fig. 7); this is particularly true of smaller *L. humilis*. This variation emphasizes the futility of basing species characters on the shell alone. Hubendick (*l.c.*) found that the shell-width/shell-length ratio of *L. peregra* showed on the average only a weak increase with an increase in shell-length. His results were based on several populations. The results of DeWitt (1954) showed that *P. gyrina* became more elongate up to the end of the first 14 weeks of growth in the laboratory, when the shell is about 12 mm. in length. Although a small amount of growth occurred after the 14th week, it was in a lateral direction with a noticeable flaring of the outer lip of the shell. A corresponding lateral growth in larger shells of *L. humilis* does not occur. The aperture-length/shell-length relation also changes with an increment in shell length (Fig. 8). At first it rises slightly and then gradually decreases. Hubendick (*l.c.*) found that in *L. peregra* there was a slight tendency for an increase in the value of aperture-length/shell-length with an increment in shell length.

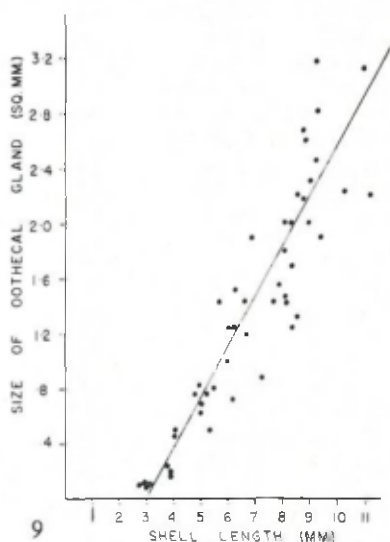


FIG. 9. The relation between oothecal gland size and shell length for *Lymnaea humilis*. The line of best fit was found to be $y = .37x - 1.10$ ($r = .906$; $R = .907$).

Figure 9 shows the relation between an increase in shell-length and an increase in size of the oothecal gland. The oothecal gland is part of the female reproductive system and is a stout cylindrical gland. In shells of the same length its dimensions vary only slightly when the animal has been properly relaxed. It was found best to use the product of the length and width of the oothecal gland as an index of size of this structure. Because of the position of this structure, it was not feasible to measure its thickness. It was also not feasible to measure this organ in shells less than 2.7 mm. long. Figure 9 shows that for the measurements made, the relation between oothecal gland-size and shell-length is a linear one, with the line of best fit found to be,

$$y = .37x - 1.10$$

As measurements were taken on shells of varying lengths, collected at

different times of the year, the ages of shells of similar lengths must have varied because of seasonal differences in growth rates. This result tends to confirm the observation that the onset of egg laying is related to size rather than age of *L. humilis*.

DISCUSSION

Results of this study indicate that *L. humilis* lives as long as nine months in the region of Ann Arbor. Snails hatched in September evidently live longer than spring broods, many of which die the following September. Van Cleave (1935) stated that the normal life span of *Fossaria modicella* (= *Lymnaea humilis*) (Hubendick, *l.c.*) varied from four to eight months and the findings of Hoff (1937) indicated that *Fossaria parva* (= *Lymnaea humilis*) (Hubendick, *l.c.*) lived 12½ to 13½ months. Both *Lymnaea haldemani* Binney and *P. gyrina* have life spans of about one year (Morrison, 1932; DeWitt, 1955).

In his study of *Fossaria modicella* Van Cleave (*l.c.*) concluded that it was probable that age and environmental conditions more effectively limited growth than did attainment of maximal size. In the present study, field observations indicated senility is related to size. *L. humilis* becomes senile when it reaches a length of nine or ten mm. and the age at which this size is attained depends upon environmental factors, primarily temperature. Hence the spring brood lives four or five months but many of those snails hatched in September or October survive until the following June. Van Cleave (*l.c.*) believed that actual size is a resultant of two main factors. Of these, growth rate is largely environmental, while length of life is probably hereditary, with seasonal influences playing a secondary role in determining length of life. In general, the findings of the present study agree with this conclusion. Undoubtedly the size at which snails die varies somewhat because in spring there is almost a five mm. variation in size of living snails two weeks prior to their death. This variation is probably due to intrinsic factors as well as to differences in the expression of environmental influences. However, growth evidently continues until death and this agrees with the findings of previous authors working with pulmonates (Hoff, 1937; DeWitt, 1955).

In April there is an initial burst of egg-laying of *L. humilis* and then a gradual decline until by June the over-wintering snails have died. Egg-laying is at its lowest ebb in June but as the spring brood becomes sexually mature it increases slightly and continues until the decline of temperature in autumn inhibits this function. Hoff (1937) stated that egg-laying in *Fossaria parva* (= *Lymnaea humilis*) (Hubendick, *l.c.*) begins about the first of April and continues for approximately one month. According to Van Cleave (*l.c.*) *Fossaria modicella* (= *Lymnaea humilis*) (Hubendick, *l.c.*) produces two new generations a year, one in March and the other in late July or early August, and each generation produces but one set of eggs. Although it is possible to divide oviposition of *L. humilis* into distinct spring and summer phases, the evidence indicates that it is a continuous process except for a possible brief cessation in June just after over-wintering snails have died.

There is little indication that *L. humilis* hibernates. Only one snail which had a diaphragm (epiphragm) was found in mid-winter (February) and this was at the Newburg locality. Mozley (1932) and Kenk (1949) found that as a pond dries in June, *L. palustris* in northern Canada and in Michigan secrete a diaphragm across the aperture and remain dormant

on the bottom of the pond, in cracks and small depressions. Hoff (1936) found that *Fossaria parva* lived almost entirely in water from December to March. As soon as ice began to form, he observed that each increase in thickness caused the migration of snails to deeper water. When a partial thaw occurred, the snail returned to more shallow water. In the present study, there was no evidence of similar movements of *L. humilis* with temperature changes in winter.

SUMMARY

1. *L. humilis* lives as long as nine months in the region of Ann Arbor, Michigan. In the field, this snail becomes senile when it reaches a length of nine or ten mm., and the age at which this size is reached depends upon environmental factors.

2. Oviposition occurs at the land-water junction, both in and out of water, but the greatest number of egg masses was always seen on land along a narrow region adjacent to the shoreline.

3. Although it was possible to divide the period of oviposition into distinct spring and summer phases, the evidence indicates that ovipositing by *L. humilis* is a continuous process, except possibly for a brief cessation in June just after over-wintering snails have died.

4. *L. humilis* did not oviposit until it reached a length of four mm. Mating snails were not observed in the field but were seen in the laboratory. In April about 95 percent of *L. humilis* were mature.

5. Egg masses varied in shape from ovoid, to reniform and curved-elongate, and the average number of eggs per mass was ten. Hatching time depended on temperature and in the laboratory occurred in about ten days.

6. Growth of young *L. humilis* was rapid; in the Clinton locality they increased in shell-length at the rate of seven percent per day reaching maturity in about 22 days.

7. The concentration of *L. humilis* on a mud flat varied seasonally. It was highest in late summer and early autumn when concentrations of 220 per sq. dm. were present.

8. With the onset of winter conditions a large number of *L. humilis* died; most of these were four to five mm. long. Smaller snails were able to survive the change from autumn to winter conditions better than larger forms.

9. There was little evidence that *L. humilis* hibernates. Only one snail was found with a diaphragm (epiphragm), and none were seen to burrow in mud.

10. Measurements of the shell showed that there is a pronounced decrease in the width-length ratio of the shell with an increase in shell length of a population of *L. humilis*.

11. The relation between an increase in size of the oothecal gland and an increase in shell length of *L. humilis* is a linear one.

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