THE ECOLOGY AND LIFE HISTORY OF THE POND SNAIL *PHYSA GYRINA*[1]

Robert M. DeWitt
Department of Zoology, University of Michigan, Ann Arbor, Michigan

Snails form an important part of the fauna of both temporary and permanent ponds. The presence of several species common to both types of habitats indicates the extent to which these animals adapt to extreme environmental conditions. The annual sequence of events in a population of a single species of snail, living in ponds, has not been accurately documented. This paper deals with such a study in the case of *Physa gyrina* Say, a typical inhabitant of temporary and permanent ponds. Populations in three localities were studied; a permanent and a temporary pond in the vicinity of Ann Arbor, Michigan and a permanent pond 300 miles to the north. Periodic collections were made to determine growth and reproduction as limited by various factors in the field and experiments were carried on to obtain information on these aspects under laboratory conditions. In the permanent situations some of the population was active throughout the year, while in the temporary habitat the life cycle was considerably altered by an extended period of dryness. This paper will consider the natural populations studied in the field; the experimental portion will be considered elsewhere.

Kenk's Pond, a temporary Habitat

The pond studied over a period of two years during this investigation was first described by Kenk (1949) and designated Pond II. It is usually 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 the 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 underlain by a clay soil.

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

Lymnaea palustris (Müller)—abundant; *Physa gyrina* Say—abundant; *Helisoma trivolvis* (Say)—common; *Gyraulus parvus* (Say)—common; *Planorbula armigera* (Say)—common.

In addition to the 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 the pond in March, 1951. These land snails are never typical of such situations during the summer and were collected here after the ice cover had disappeared at which time the water temperature was 7° C.

Scio Pond, a permanent Habitat

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. During late fall and spring, it 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 direct communication with the river, and an eastern part into which river water still freely passes. The isolated portion is about 12 by 20 feet and one foot in depth during the driest period of the year.

The pond is densely shaded by a large number of elms and willows mixed with a few maples. In contrast to Kenk's pond, no Typha is present 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. By far the most abaundant aquatic vegetation is filamentous algae, which grows in large masses. The bottom of the western portion is thickly covered with leaves under which lies a layer of black muck mixed with brown, peaty material. The bottom of the eastern portion, subjected to action of river currents, is relatively free from accumulated plant debris and consists of

[1] This material was included in a thesis completed under the direction of Professor F. E. Eggleton and submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, University of Michigan, Ann Arbor.

muddy sand, coarse gravel, cobble stones and boulders. The population 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 gastropod fauna is quite different from the association found in a temporary pond. Both typical river forms and those associated with backwaters are found here.

The Streptoneura found were *Campeloma decisum* (Say)—abundant; *Valvata tricarinata* (Say)—common; *Amnicola limosa* (Say)—common; and *Amnicola lustrica* Pilsbry—common. Pulmonata found were *Lymnaea palustris* (Müller)—common; *Lymnaea obrussa* Say—abundant; *Lymnaea humilis* Say—common; *Physa gyrina* Say—abundant; *Helisoma trivolvis* (Say)—common; *Planorbula armigera* (Say)—common; and *Ferrissia rivularis* (Say)—rare.

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 late 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 at Scio meets these requirements and a large population has established itself.

The presence of two species of *Amnicola* is not unusual. They are tolerant of a wide range of natural habitats being found in creeks, rivers, and fresh- and brackish-water lakes (Berry 1943). *Valvata* has also been reported from a diversity of habitats (Baker 1928) and during this investigation has been encountered in a variety of 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 and *L. obrussa* and *L. humilis* are frequently found in association with them. Temporariness of habitat is certainly not a requisite for completion of the life cycle of these snails, rather it is a factor to which they have successfully adapted.

The typical stream form, *Ferrissia,* is not well established in the pool and its presence is probably accidental.

With reduction of temperature in the fall a third assemblage of species, the terrestrial pulmonates, makes its appearance. *Deroceras laeve* has consistently been present in winter collections from temporary and permanent ponds. These slugs are able to survive several months' submergence. Pearl (1902) reports that this slug crawls into water as the temperature drops and leaves it as temperatures rise. These facts indicate that this is probably a part of the normal behavior in certain slugs. Other terrestrial species, *Succinea* and *Zonitoides,* have been recovered from similar situations.

Life Cycle

Kenk's Pond

Physa gyrina began to oviposit in April when the temperature of the water had risen to at least 10° C.; the eggs hatched in from eight to ten days. Juveniles fed continuously and as the pond began to dry moved toward the center where water remained longest. Before all standing water had disappeared, the immature snails burrowed into the relatively soft bottom and remained there until the fall rains filled the pond. Then the snails came out of the bottom deposits and began to movè about and feed. As the water temperature lowered during the fall, the snails were increasingly less active. During the winter they moved very slowly under the ice or remained motionless for long periods of time. Some growth must have occurred during the winter months because mature snails which were scarce in the fall, predominated in spring collections.

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 January. Although *P. gyrina* were present in March of 1951 they were less abundant than in the preceding year when the pond was filled in November.

Scio Pond

Field observations and collections of *P. gyrina* were made in the western portion of the pond. Although subject to the greatest fluctuations of water level, this area supported the largest numbers of these snails. While the water temperature ranged from 1.5 to 3° C. the population was concentrated in deeper (3-4 feet) water. As the temperature rose, the snails moved to shallower (2-6 inches) portions of the pond.

As in Kenk's pond, temperature appears to be the factor controlling oviposition. In April, when the water temperature was above 10° C., the population consisted almost entirely of sexually mature individuals which began to oviposit. In May the adult population had been virtually replaced by juveniles. Egg masses were relatively scarce.

Throughout the remaining warm months (June through October) no snails were observed in copulation and no egg masses were found in the field. From August on the population contained a high percentage of individuals within the size range of snails which oviposited in the spring. Some of those collected in August and succeeding months laid eggs when brought into the laboratory. These were snails born in the spring which were sexually mature by late summer or early fall of that year. The second generation they produced did not mature until after May of the following year. This accounts for the few juveniles present in the population following May and the few adults observed in May.

Neither laboratory raised nor field collected snails from Scio oviposited before reaching 7 mm in length. Observations made on 60 snails indicates that length is the most reliable index of sexual maturity. All snails (from the Scio population) 7 mm or over are considered to be capable of ovipositing under favorable environmental conditions. Relative proportions of sexually immature and mature *P. gyrina* over a complete annual cycle are given in Figure 1.

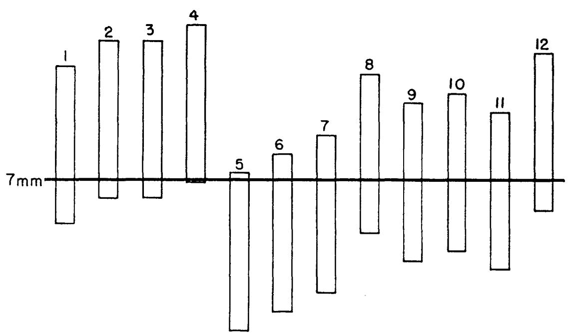

FIG. 1. Per cent of sexually immature and mature *Physa gyrina* within each month's collection from Scio. The numbers refer to the month in which the collection was made.

Most of the parent generation died during the month of April following a burst of oviposition. In May the population was composed almost exclusively of newly hatched individuals measuring from one to three mm in length. Various combinations of factors contributed to the disappearance of uniformity within the population during the succeeding months (Fig. 2). Early growth is so rapid (DeWitt *in press*) that age differences between broods laid by a single parent may be prominent and the effect of differential growth rates together with localized environmental inhibitors and stimuli contribute to this heterogeneity. In addition, a small number of ovipositing individuals were present in May and June. From November to April oviposition ceased and although growth was retarded by low temperature there was a general increase in the mean size of the population.

Black River Pond

This pond, a backwater of the Black River, is located in Cheboygan County about 300 miles north of Ann Arbor. In most respects it resembles the Scio locality. It was visited in mid-May and a collection of mature *P. gyrina* was made. At this time, large numbers of egg masses were present on submerged vegetation and many snails were in copulation.

One month later the population had changed radically; juveniles predominated, only a few individuals of adult 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 mean size each month.

DISCUSSION

Under relatively stable laboratory conditions, *Physa gyrina* may live as long as 22 months. There is no indication that a rest period is essential to growth or activity. Laboratory-reared snails successively undergo developmental, reproductive and post-reproductive periods and are not subjected to such fluctuating environmental factors as temperature, desiccation, parasitism, anaerobiosis and food supply, as they would be in a natural habitat. In permanent ponds, the life cycle extends over 12 to 13 months while those populations in temporary ponds may live for an additional six months.

None of the snails living in temporary ponds are restricted to these habitats but have developed a tolerance to limited desiccation. Survival in such an environment may be accomplished in several ways. Baker (1914) thought that failure to find living snails during dry periods indicated that the egg masses were resistant to desiccation. In Kenk's pond, however, immature *P. gyrina* were estivating in dry bottom materials. Mozley (1932) reported that *Lymnaea palustris* formed an epiphragm during the dry season; such a structure was not observed in any *P. gyrina*. From my observations it appears that immature snails, perhaps because of area of exposed surface, are more resistant to drought than are adults. Cheatum (1934) demonstrated that the resistance of temporary pond species to desiccation is greater than that of lake pulmonates. Estivation forced upon *P. gyrina* in temporary ponds delays growth and the snails hatching in the spring rarely at-

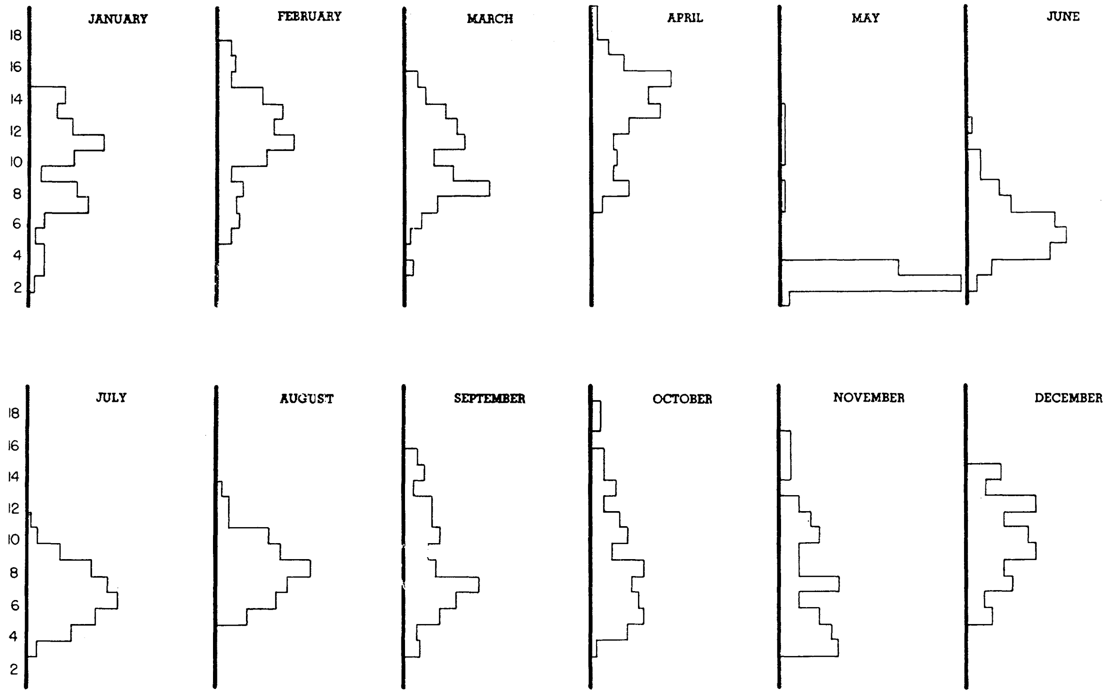

FIG. 2. Monthly collections of *Physa gyrina* from Scio plotted according to the percentage of individuals falling within certain size-class limits. The numbers represent the length of the shell in millimeters.

tain sexual maturity by the fall of the same year as do individuals living in permanent ponds. The length of the dry season can alter the life cycle. If long enough, there is not enough time in the spring for the animals to become sexually mature and they may overwinter a second year.

In both habitats, temperature is the critical factor controlling overt reproductive behavior. Copulation and oviposition do not take place until the water temperature has reached 10 to 12° C. Although sexually mature individuals were very common in Scio pond from early fall through winter, large numbers of egg masses were not present until spring. A few individuals born in the spring did become sexually mature by late summer and these oviposited as long as the temperature remained at or above the critical point. Sexually mature snails were present in Kenk's pond only in the spring. This temperature-controlled reproductive pattern is not present in laboratory reared snails. They begin to oviposit at the end of the developmental period regardless of the season. Similar conditions were approximated in a stream in Illinois fed by warm waste waters in which *P. gyrina* lived and oviposited continuously irrespective of air temperatures (Agersborg 1932).

Severe anaerobic conditions may result in death of a large number of individuals within a population but such conditions are probably more frequently encountered in temporary than in permanent waters. It has been demonstrated experimentally that *P. gyrina* possesses a limited anaerobic resistance (Von Brand, Baernstein, and Mehlman 1950) and I have taken these snails alive from bottom deposits in temporary ponds when hydrogen sulfide was so abundant that its odor was detected as soon as the ice cover had been broken. The water immediately under the ice contained 3.2 ppm of free oxygen but this quantity would steadily decrease as the bottom of the pond was approached. These conditions exist only when ice covers the ponds and Alsterberg (1930) has shown that snails kept anaerobically at from 0 to 10° C. live three times as long as those kept at 20°. In addition, chemical and physical factors are so varied within a given habitat, that snails, which are capable of moving from one microhabitat to another, quite possibly do not have to undergo an extended absence of free oxygen.

Most of the food supply in temporary ponds is derived from terrestrial plants; permanent ponds are likely to support a flora of aquatic flowering plants which supplements the other sources of food. The diet of *P. gyrina* consists of dead and decaying vegetation together with living algae and water molds. Animal remains, although eaten when available, constitute a minor portion of the diet. A liberal supply of organic matter in the form of dead leaves is present in those ponds found in a wooded area; those in more open regions frequently have a portion of their margins bordered with Typha whose leaves when dead and submerged form a favorable substrate for a growth of algae and water molds. In addition, grasses and other herbaceous plants invade the bottom of temporary ponds during the dry season and furnish quantities of dead plant material when the ponds become filled.

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, which is a factor in determining composition of some populations, can be disregarded. Accidental death, due to deviations from optimal ecological conditions such as pollution, and to scarcity of food, did not appear to play a significant role within any of the populations studied.

Species in temporary ponds, incapable of leaving such an environment, are subjected to factors causing high mortality within the population. These habitats are highly selective and species living here are likely to become genetically homogeneous at a more rapid rate than those which can migrate or which live in a less rigorous habitat.

Summary

Physa gyrina is a typical inhabitant of temporary and permanent ponds. The life history and ecology of this pulmonate snail were studied in three ponds in Michigan. In a permanent pond in southern Michigan, oviposition occurred in the spring when water temperatures reached 10 to 12° C. 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. Within the Scio population a shell length of seven mm was determined to be the size below which snails are believed to be sexually immature. Those individuals seven or more millimeters in length are capable of ovipositing under favorable environmental conditions. The life span of individuals in the field is from twelve to thirteen months. The life history of *P. gyrina* in a permanent pond 300 miles north of the above-mentioned habitat differed only in that oviposition took place three to four weeks later in the spring.

Temporary ponds, located in southern Michigan, are usually dry from mid-June until November. Estivation forced upon *P. gyrina* living in such habitats delays growth, and the snails 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. If the dry period is unusually long, the snails may overwinter a second year. Thus the life span in such situations may be considerably longer than in permanent ponds.

References

Agersborg, H. P. K. 1932. The relation of temperature to continuous reproduction in the pulmonate snail, *physa gyrina* Say. Nautilus, **45**: 121-123.

Alsterberg, G. 1930. Wichtige Züge in der Biologie der Süsswassergastropoden. Lund. (paper not seen).

Baker, F. C. 1928. The fresh water Mollusca of Wisconsin. Part I. The Gastropoda. Wisc. Geol. & Nat. Hist. Surv., Bull. 70, 507 pp.

Baker, H. B. 1914. Physiographic and molluscan succession in lake pools. Mich. Acad. Sci., Rep., **16**: 18-45.

Berry, E. G. 1943. The Amnicolidae of Michigan: distribution, ecology and taxonomy. Misc. Pub. Mus. Zool., Univ. Mich., 57, 68 pp.

Cheatum, E. P. 1934. Limnological investigations on respiration, annual migratory cycle, and other related phenomena in freshwater pulmonate snails. Trans. Amer. Micros. Soc., **53**: 348-407.

Goodrich, C. 1932. The Mollusca of Michigan. Univ. Mich., Univ. Mus. Handbook Ser., **5**, 120 pp.

Kenk, R. 1949. The animal life of temporary and permanent ponds in southern Michigan. Misc. Pub. Mus. Zool., Univ. Mich., **71**, 66 pp.

Mozley, A. 1932. A biological survey of a temporary pond in northern Canada. Amer. Nat., **66**: 235-249.

Pearl, R. 1902. A curious habit of the slug *Agriolimax*. Mich. Acad. Sci., Rep., **3**: 75-76.

Von Brand, T., H. D. Baernstein and B. Mehlman. 1950. Studies on the anaerobic metabolism and the aerobic carbohydrate consumption of some fresh water snails. Biol. Bull., **98**: 266-276.