

COMPARATIVE STUDIES ON THE LIFE CYCLE AND ECOLOGY OF TWO POPULATIONS OF *PHYSA HETEROSTROPHA* (SAY) (GASTROPODA: PULMONATA)¹

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Two populations of *Physa heterostropha* Say (Pulmonata: Gastropoda) were observed during 1971 near Cooperstown, Otsego Co., N. Y. The study was conducted in an Otsego Lake embayment (Rat Cove) and a small lake (Moe Pond) on the lands of the Oneonta Biological Field Station. *P. heterostropha* began ovipositing in June in both habitats. Both populations exhibited two cohorts (distinct age groups appearing at different times) one hatching during June and July and the other in August, September, and October. Growth rate data show slower increases in weight with maturity and slower growth when water temperatures were lower, in the fall. There was an inverse relationship between total egg production and population density. The number of eggs oviposited per egg mass appeared to be predominantly influenced by the age of the adults. High mortality (greater than 1%) was attributed to physical stresses such as wave action, dessication and ice cover, and predation. The leech, *Helobdella stagnalis* (L.), was predatory on populations in Moe Pond. *Dugesia tigrina* (Girard) and *H. stagnalis* preyed on *P. heterostropha* in Rat Cove. Populations of these organisms increased greatly one to four weeks after snail populations exhibited high densities, reflecting the density dependent characteristics of typical prey specific predators.

Snails are vectors of trematode parasites which affect man and other vertebrates. With increased construction of reservoirs and irrigation systems throughout the world, gastropods have increased their ranges and population densities. Concomitant with this has been an increase in the range of gastropod parasites. More information about life cycles of freshwater pulmonate snails is therefore of value to those concerned with snail control.

The immediate goal of this study was to increase our knowledge of *P. heterostropha*. The most pertinent papers con-

cerning population dynamics of the genus *Physa* were those of Dewitt (1954, 1955) and Clampitt (1970) on the related species *P. gyrina* Say and *P. integra* Halde- man. The only reference dealing with the life cycle of *P. heterostropha* was written by Wurtz (1949).

Physa heterostropha populations were studied in two areas located in Otsego County, near the headwaters of the Susquehanna River at Cooperstown. Rat Cove, located on the southwestern shore of Otsego Lake, is roughly 0.4 x 0.2 km in size, up to 6 m in depth and possesses a bottom composed of deep (<1 m) organic muds in the littoral areas. On this substrate grows a dense cover of more than 30 species of aquatic macrophytes (Harman and Doane, 1970). The cove is bordered north and south by two small points and is somewhat protected from the full force of the waves.

The shoreline, where populations of snails were studied, is composed of large cobbles (3-20 cm in diameter) overlying gravel and sand. The main source of this rocky substrate is glacial till. The rocks are cleansed constantly by the action of waves and few macrophytes grow in the area. Wave action however, often causes plant debris to wash up on the shoreline. A deciduous wooded slope rising above the shoreline at an angle of approximately 35° contributes deciduous leaves to the plant material which accumulates at the shore during the autumn months. Ice covered the lake from December through April 1971. During June and July the water receded 0.2-0.4 m, exposing more of the inorganic substrate.

Some of the ecologically important associates found with *P. heterostropha* in this habitat are the snails *Lymnaea humilis* (Say) and *Gyraulus parvus* (Say). Populations of other aquatic inverte-

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brates typical of lentic biotopes are present including the gastropod predators *Helobdella stagnalis* (L.) (Annelida: Hirudinea) and *Dugestia tigrina* (Girard) (Platyhelminthes: Turbellaria).

The second population studied was at Moe Pond, a small, artificial, eutrophic lake 1.5 km to the west of the Otsego Lake collection area. The pond has a width of 330 m, a length of 750 m and its greatest depth is 3.7 m. Most aquatic macrophytes are restricted to waters 0–12 cm in depth, probably because of shallow compensation points resulting from algae laden water. There were algal blooms at Moe Pond in August and September. Floating clumps of mucilaginous algae obscured the substrate in several areas of the transect in late August.

The collection area, located on the southwest shore of the pond, includes water 0.10 cm deep in a 60 m long strip adjacent to the shore. Substrate in the area is mostly flattened stones, silt and sand derived from Devonian shales and glacial deposits. A layer, 1–4 mm thick, of silt and aufwuchs covers the rocks. Submergent *Eleocharis* sp. and *Chara* sp. grow in patches on the silt substrate and *Carex* sp. is emergent at the shoreline. The terrestrial area adjacent to the collection site is old field. Sensitive fern (*Onoclea sensibilis*) rhizomes and roots form a low bank which projects into the water along the northern half of the transect. The remainder of the bank supports grasses and common weeds. Important associates included the pulmonate limpet *Ferrissia parallela* Halde-man and many populations of aquatic Arthropoda. Also present are *H. stagnalis* and another leech, *Placobdella* sp.

The water level was highest in the spring, but receded quite rapidly after May, exposing 0.1–0.4 m of inorganic and organic substrate. Because of the ponds small surface area and protection from the wind, waves rarely attained a height greater than 5 cm. Ice covered the water from late December 1970 to late April 1971.

METHODS

For designation of sample areas, uniform intervals were marked along transects at each collection site. These transects were parallel

to the shoreline and were about one meter wide. The Moe Pond transect was 60 m long and had 3 m intervals. The Rat Cove site was 23 m long and was composed of 1 m intervals. Numbers generated from a computer random number program (APL) determined which interval was to be sampled at each of the collection sites during each sampling period.

Areas in each transect were sampled once a week. Population growth is slower in the winter under ice cover (Dewitt 1955, Duncan 1959 and McCraw 1961), so similar samples were taken once each month during winter. In each area a square metal frame, 21.5 cm on each side (462 cm²) and 11 cm high, was placed in the water at depths from 0–10 cm to delineate the areas to be sampled. Also used for sampling were two 21.5 cm rods placed 21.5 cm apart to form a square. This method proved more satisfactory in microhabitats where the sample area was not shaded by the high sides of the metal frame. All stones inside the area outlined by the metal frame, or rods, were picked up and inspected visually for snails and their eggs. The total number of snails and eggs for each sample was noted. When there were many immature snails present in populations found on silt and fine gravel substrates, those materials were scooped up and placed in a 75 ml beaker filled with water so that they could be inspected with a 2.5× hand lens. When vegetation was dense enough to obscure inorganic substrates, a 115 cm² subsample of substrate and vegetation out of the 462 cm² area was removed and returned to the laboratory. Snails were collected from the vegetation using a dissecting microscope.

Several randomly placed small samples were more reliable than one large sample because of the clumping that occurs in natural populations. Each sample contained 0 to 27 snails, similar to the 3 to 20 individuals per sample that satisfactorily represent the density of snail populations (Hariston *et al.*, 1958). At Moe Pond it was impossible to take valid samples after ice formed because the water was frozen completely to the substrate in the collection area.

Height-width data were collected and analyzed using the methods of Sokal and Rohlf (1969) to show annual changes in shell morphology of the species studied, and to compare morphological differences between the two populations. Snails found inside the transect were returned to the water as soon as they were measured to assure minimal disturbance of the populations. The percentage of egg survival from the prelarval (newly laid) to protoconch stage (immediately before hatching) was based on the numbers of eggs per egg mass at various stages of development.

Air and water temperatures were recorded on each sample date. In Rat Cove all temperature readings were taken between 12 a.m. and 2 p.m. Temperature measurements at Moe Pond were usually taken between 9 and 11 a.m. Daily or weekly maximum and minimum temperatures were recorded in both locations and showed a 3°–10°C variation from noon of one

day to the following morning and a 5°–15°C variation weekly.

Water samples were analyzed for pH using a Beckman pH meter. The Alsterberg modification of the Winkler method was used for determination of dissolved oxygen. Total alkalinity in ppm as CaCO₃ was determined by titration with 0.02N H₂SO₄ using methyl orange as the indicator (Amer. Pub. Health Assn., 1971). A nomograph was used to calculate CO₂ ppm (Moore 1939).

ments for *P. heterostropha*, all of the snails in each sample were placed in the following size classes: 0.5–1.4, 1.5–2.4 mm, etc. to 15.4 mm. The data from each collection date represent the average of five samples, except during winter months when an average of three samples was used.

The total numbers of eggs and numbers

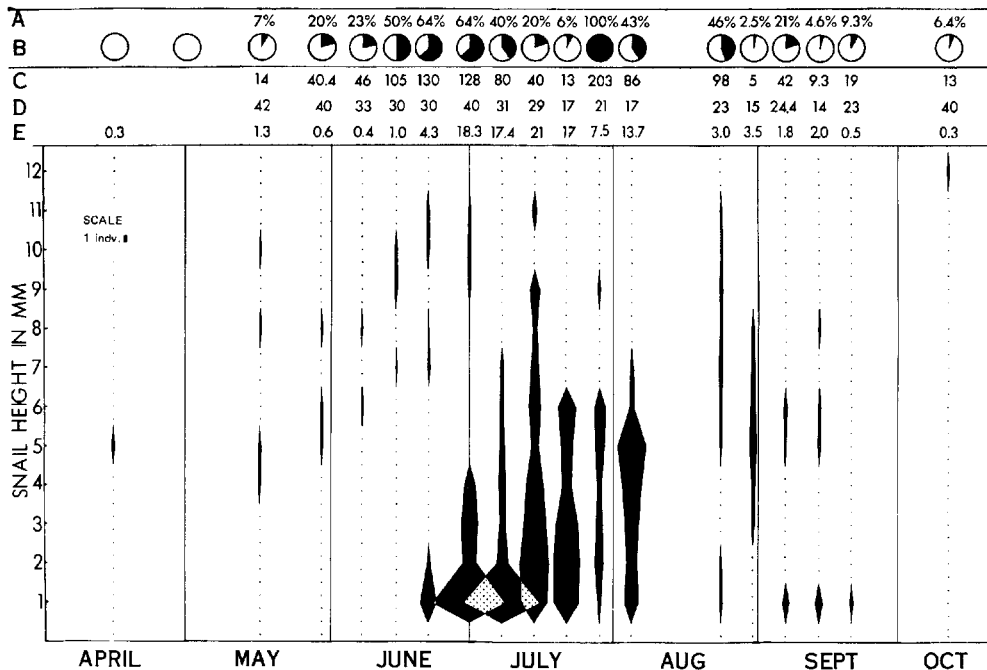


FIGURE 1. *Physa heterostropha* in Rat Cove. The size classes are on the ordinate and the number of snails in each size class is represented by the width of the vertical line.

Row A. Relative number of eggs collected. Percentages based on 100% representing the maximum number of eggs collected in any one sample during the study period

Row B. Diagrammatically illustrates data in Row A

Row C. Average number of eggs present

Row D. Average number of eggs per egg mass present

Row E. Average number of snails and eggs present per sample.

RESULTS

Population characteristics. Regression lines computed from height-width measurements indicated that the shells of *P. heterostropha* in Rat Cove had a somewhat greater height-to-width ratio than those in the Moe Pond populations, resulting in a more obese adult morphology. Weekly changes in populations during the sample period are shown as histograms (figs. 1 and 2) (Hunter 1961a, b, Duncan 1959). Using height measure-

of eggs per mass oviposited by the snails was influenced by environmental and genetic factors, (figs. 1 and 2), this information is important in ascertaining mortality and natality rates for each population and in determining if the populations were density dependent. Each egg mass was counted, with the total estimated to the nearest five eggs. The stage of development; prelarval (0.2 mm), larval (0.4–0.5 mm) and possession of a protoconch (0.8 mm) also was noted. Since

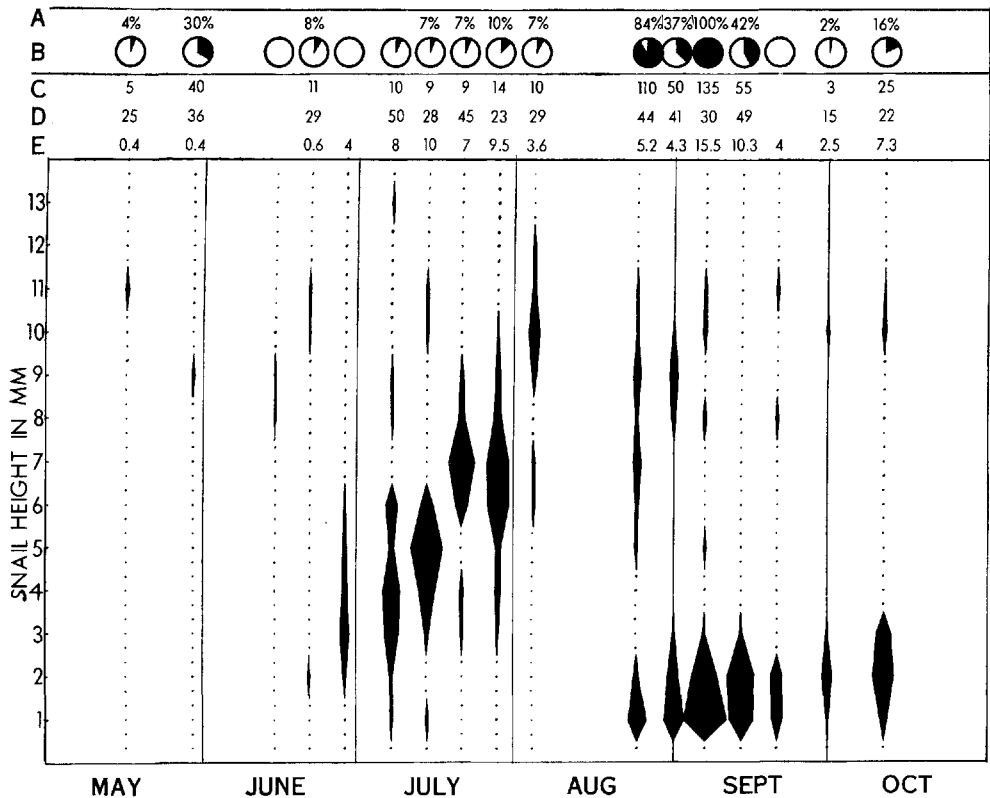


FIGURE 2. *Physa heterostropha* in Moe Pond. The size classes are on the ordinate and the number of snails in each size class is represented by the width of the vertical line using the same scale shown in figure 1.

- Row A. Relative number of eggs collected. Percentages based on 100% representing the maximum number of eggs collected in any one sample during the study period.
- Row B. Digrammatically illustrates data in Row A.
- Row C. Average number of eggs present.
- Row D. Average number of eggs per egg mass present.
- Row E. Average number of snails and eggs present per sample.

prelarval eggs observed at week X would also be present at week X+1, eggs in the protoconch stage at week X+1 were not included in the total egg count for that week. The percentage of survival of eggs was computed from data representing the differences in averages of eggs per mass between prelarval and protoconch stages of development.

Height-weight regressions (Sokal and Rohlf 1969) were used to obtain biomass and growth rate statistics (fig. 3, 4), because during routine sampling only the dimensions of the organisms were recorded. It was necessary to use this technique to keep disturbances in the

sample area at a minimum (Eckblad 1971a). One hundred *P. heterostropha* were collected for size-weight (wet weight of shell and soft parts) measurements from areas adjacent to the transects. Analysis of each regression line indicated three different slopes evident at various periods during development.

The growth rate (r) reflects changes in weight (W) of a cohort as it develops over a time interval (t). The equation used to calculate these growth rates was $r = (\log W_t - \log W_0) \div t$ (Eckblad 1971b). From the size-frequency histograms several cohorts were chosen and traced from 0.5 mm to 12 mm. The size class of

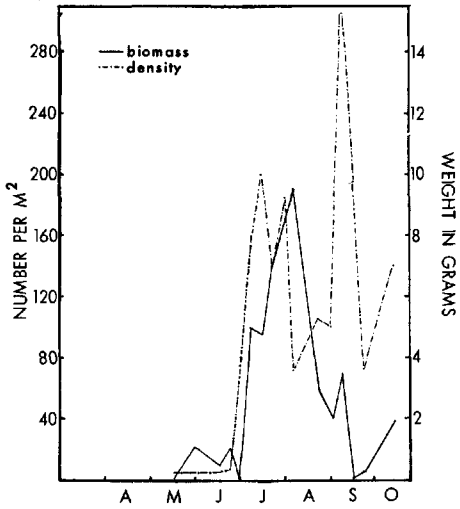


FIGURE 3. Biomass-density of *Physa heterostropha* in Rat Cove (April to October).

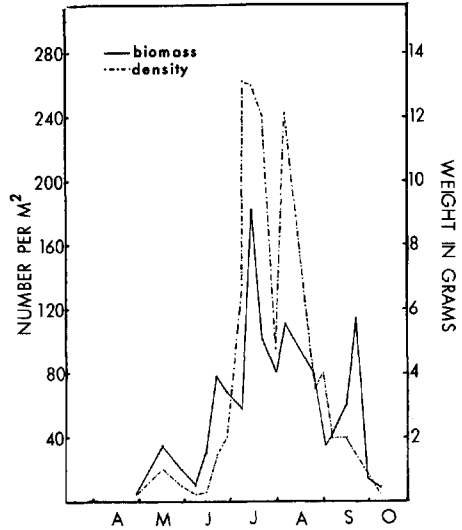


FIGURE 4. Biomass-density of *Physa heterostropha* in Moe Pond (April to October).

each cohort on each sample date was determined, and its weight was ascertained from the size-weight regression line. Attempts to obtain growth rates from the Rat Cove population were difficult because the cohorts were not always clearly defined. Figures 5 and 6 illustrate the growth rates of both populations.

Rat Cove: The first snails adequately sampled in Rat Cove were noted in May 1971 (fig. 1). Two groups of overwintering snails were 3.5–5.4 mm and 8.5–11.4 mm in height. The smaller snails grew rapidly and reached 7.5–9.4 mm in height by the middle of June, attaining the size of the first, so the two groups could no longer be recognized after that date.

Oviposition began in mid-May and

continued until mid-October (fig. 1). The egg production was bimodal, with the greatest numbers oviposited in late June and the first week in July, and in the first week of August. From June 21 to September 20 there was a small, but constant, addition of new snails. Snails hatching in June and early July reached 8.5–9.4 mm in height and started to oviposit by late August. The adults that overwintered in 1970 (as determined by shell morphology) were not observed after July 1971. Snails hatching in August developed to about 4.5–6.4 mm in height before winter. The small group hatching in September could not be traced past the first size class (0.5–1.4 mm in height). Two groups, 0.5–1.4 mm and 4.5–8.4 mm in height in September, overwintered in 1971.

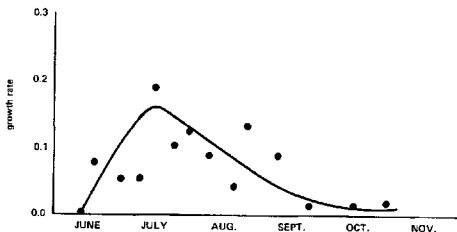


FIGURE 5. Growth (grams/day) of *Physa heterostropha* in Rat Cove.

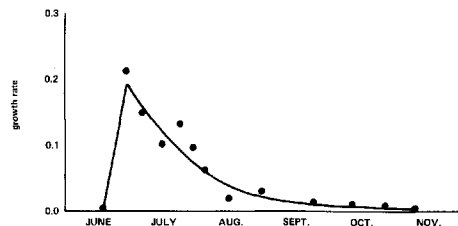


FIGURE 6. Growth (grams/day) of *Physa heterostropha* in Moe Pond.

The survival rate, from eggs from oviposition to adult was 0.3% (most snails in this population become reproductively viable when they attain 8.5 mm in height), and from young to adult the survival rate was also 0.3%.

Moe Pond: Figure 2 illustrates the life cycle of *P. heterostropha* at Moe Pond. One cohort was present in May 1971, and snails began to oviposit the last week of May. Two weeks later the first young appeared. The larger overwintering population disappeared by the first of July and the smaller cohort reached near maximum sizes (10.5–12.4 mm in height) by mid-July. This cohort reached 9.5–11.4 mm in height during the first two weeks in August. By mid-September less than one individual per sample was found. The second oviposition period occurred during the third week of August and the first week of September. The resulting cohort appeared August 23, with the most intensive hatching occurring in the first and second weeks of September. During the second half of September the cohort grew slowly and did not reach the larger size classes (3.5 mm in height or greater). By October only a few adults 8.5 to 10.4 mm in height had survived. Several adults were collected from outside the sample area that were recorded from 10.4 to 13.5 mm in height. Survival rate from eggs to adults was 0.28% and from young to adults 7.8%.

During the reproductive periods the populations studied exhibited weekly variations in average eggs per mass. The average eggs per mass of *P. heterostropha* at Rat Cove (fig. 1) was greatest when overwintering adults deposited their first eggs in May. It then decreased as these older snails completed growth and died in July, and as the population numbers increased. Lower average eggs per mass occurred in July and early August when the population was most dense (17–21 per sample) and the first cohort (8.5–9.4 mm in height) was beginning to oviposit. The average numbers of eggs per mass increased after eight weeks.

In Moe Pond (fig. 2) *P. heterostropha* egg masses with the largest average numbers of eggs ($\bar{X}=50$) were found after five weeks of oviposition when the overwintering adults were near maximum

sizes and when the first cohort of the 1971 hatch reached high densities. There were fewer eggs per mass ($\bar{X}=23$) in late July before the first cohort reached maturity, the overwintering adults were dying, and the density of the first cohort had been at its highest for four weeks. The first cohort produced the largest number of eggs per mass ($\bar{X}=49$) five weeks after it began ovipositing and when the first and second cohorts combined had already attained their greatest density. Egg-per-mass averages were lowest at the end of the reproductive period in late September and October. The percentage of egg survival from the prelarval to protoconch stage was 45% in Rat Cove and 56% in Moe Pond.

Total eggs produced by overwintering adults and spring cohorts of *P. heterostropha* varied throughout the reproductive periods. Egg production by overwintering adults in Rat Cove showed the largest number of eggs in late June, four weeks after oviposition began. The numbers decreased during July when adults were dying and the snail densities were highest. It increased again when the first cohort began ovipositing, but total production declined from August to October as population density decreased.

Eggs in Moe Pond laid by overwintering adults were most numerous in May when the snail density was low (1 or less per sample). The number decreased with increasing numbers (40–50 per sample) of newly hatched snails. The populations of *P. heterostropha* in Rat Cove laid about twice as many eggs per unit area sampled over the summer period as those at Moe Pond.

Populations of *P. heterostropha* in Moe Pond exhibited a higher density during most of the summer than did the populations in Rat Cove (figs. 3 and 4). In 1971 a few overwintering adults added to total biomass until they died July 28 at the end of their 12–14 month life span. Density increased from 7 to 262/m² from mid-June to mid-July and decreased after August 4 from 243 to 5/m². Biomass however, increased from 1.75 to 5.7 g/m² a second time in mid-September due to the growth of the August 20 cohort. The density and biomass were the highest (262/m², 9.1 g/m²) in mid-July because

there were many snails in nearly all the size classes. Biomass averaged 3.1 g/m² and density 58.5/m² in 1971.

Basic changes in Moe Pond were similar to those of the Rat Cove population (fig. 4). In June 1971 there were few adults and both density and biomass were reduced (5/m², 0.7 g/m²). These values increased to 200/m², 9.5 g/m² in July and then decreased to 71/m², 2.0 g/m² in the first two weeks of August. A decrease in population density indicated mortality with few replacements by young snails. The increased density (305/m²) and biomass (3.5 g/m²) in September indicated the hatching of a second cohort.

Growth rates were highest in June and July and gradually declined to near zero in October and November. *Physa heterostropha* in Moe Pond grew at its greatest rate in June and July, but after late July grew at a slower pace until they practically ceased in November (fig. 6). The population in Rat Cove exhibited similar growth rates (fig. 5) with the exception of a higher total growth rate (0.88 g/day) than at Moe Pond (0.82 g/day). The Moe Pond snails reached maximum growth three weeks sooner than those in Rat Cove.

Physical and chemical parameters. Temperature measurements at Moe Pond, usually taken between 9 and 11 a.m., fluctuated greatly. In 1971 Moe Pond warmed from 5° to 21°C in less than one month. The same temperature increase took 6 weeks in Rat Cove. The warmest stable summer temperatures in Moe Pond and Rat Cove were 22°C and 21°C respectively.

Oxygen values fluctuated between 7 and 11 ppm in Rat Cove and between 3.8 and 8.2 ppm in Moe Pond during the study. At Moe Pond the pH values showed greater extremes than those in Rat Cove and were highest in June and September (8.2-8.7). The lowest reading (7.3) was taken in August. Changes in alkalinity paralleled pH changes. The highest alkalinity values (Rat Cove: 105 to 122 ppm, Moe Pond: 38 to 40 ppm) were present in June, and the lowest (Rat Cove: 75 ppm, Moe Pond: 19 ppm) were recorded in August.

Predator populations. Some leeches

(Annelida: Hirudinea) and flatworms (Platyhelminthes: Turbellaria) are predaceous on snails (Mann 1955, 1961). Three leeches, *Helobdella stagnalis* (L.), *Placobdella* sp. and *Nepheleopsis obscura* (Verrill); and one flatworm, *Dugesia tigrina* (Girard), were present in the biotopes studied. *Helobdella stagnalis* was abundant in both Rat Cove and Moe Pond. *Nepheleopsis obscura* was found only in the shallowest water (1 cm) at Rat Cove, in numbers less than 0.8/m². In Moe Pond *Placobdella* was observed in shallow water in numbers less than 0.2/m². *Dugesia tigrina* occurred in both areas with populations reaching densities of 260/m² in Rat Cove during August.

In early May and late August and September of 1971 *Helobdella stagnalis* populations in Rat Cove reached their greatest densities (30/m², 25/m²). The leeches were most numerous 2 to 3 weeks after the population peak for snails. In July, an increase in *H. stagnalis* populations in Moe Pond was concurrent with the increase in the snail populations. The number of leeches per unit area declined at the end of July when snail numbers were decreasing, and increased again in August and September when the second cohort of *P. heterostropha* was hatching. Leeches and snails remained at a high density through October when sampling ended. During the summer Moe Pond leech populations were approximately four times the density of those in Rat Cove.

DISCUSSION

Freshwater pulmonate life cycles vary greatly, but in the temperate zone annual life cycles are most common (Hunter 1961a, b, Boycott 1936). In an annual life cycle snails develop, reproduce, and die in one year. Within this cycle several patterns have been observed (Dewitt 1955, Hunter 1961a, b, Duncan 1959, McGraw 1961, Geldiay 1956, Burkey 1971, Gillespie 1969). Mature members of the population may produce one, two or three cohorts (hatching at different times the same summer) or continuously produce throughout their reproductive period (Burkey 1971, Walton and Jones 1926). If there is more than one cohort, the first may be replaced or

supplemented by succeeding ones (Hunter 1961a). Some individuals produced in one summer may grow and mature before overwintering; others may near maximum sizes and mature after overwintering; or overwinter as small immature individuals which mature the following spring.

Physa heterostropha at Rat Cove and Moe Pond exhibited two cohorts per summer (June-July; August-September), the second supplementing the first. Snails in the first cohort matured before winter and those in the second cohort grew, but did not reach the largest size class, before overwintering.

Previous studies of *Physa* spp. have shown two cohorts, the second maturing after the winter (Dewitt 1955, Duncan 1959, Clampitt 1970). The periods of reproduction in *Physa gyrina* (Say) studied in Iowa (Clampitt 1970) were similar to local *P. heterostropha* populations, but other species demonstrated longer time intervals between cohorts. Variations in initiation of oviposition, development of eggs, and fecundity of adults are related to both physical and biotic factors. Dewitt (1954) and Eisenberg (1970) observed differences in reproductive responses of gastropods due to temperature, population density and nutrient availability.

The first egg masses of *P. heterostropha* were noted at Rat Cove when temperatures were near 7.5°C at noon on May 16, 1971. The Moe Pond water temperature was 14-15°C (10:00 a.m.) when *P. heterostropha* egg masses were observed May 22, 1971. If a specific temperature increase was necessary to stimulate oviposition, then 7°C above freezing was required at Rat Cove and at least 14-15°C in Moe Pond. Other species of *Physa* have been observed (Duncan 1959, Hunter 1961b) to begin ovipositing at temperatures of 10°C to 18°C.

Total eggs produced by a snail during its reproductive period appear to be more dependent on population density than any other factor (Eisenberg 1970). Egg production was highest when population densities were lowest. The fewest eggs were laid when the snails were very abundant or had reached the end of their reproductive period. During egg de-

velopment, eggs laid by *P. heterostropha* in Moe Pond had a higher survival rate (55.4%) than those in Rat Cove (44%). Eggs laid by *P. heterostropha* at Moe Pond were more viable than those in Rat Cove possibly because of more optimal nutrient supplies available to Moe Pond snails. These microphagous snails feed on decaying vascular plants and aufwuchs growing on them (Calow 1970). The aufwuchs community at the Rat Cove transect was sparse due to agitation of the cobbles by waves.

Variation in number of eggs per egg mass produced by *P. heterostropha* did not depend on population density. Fecund overwintering snails in Rat Cove produced large numbers of eggs per mass when population density was low in May and also when it was high in late June. In late July eggs per mass decreased as the snails reached senility. In late August the first cohort laid many egg masses in an apparent response to low snail densities, but there were very few eggs per mass because the individuals had not fully matured. Population density was high in September, and the first cohort produced increased eggs per mass until winter as its members reached full maturity. The most eggs per mass were observed in Moe Pond despite high population densities during the highest reproductive period of the snails. Frank (1968) suggested a selection for early maturing snails in populations when individuals reach adult stages long before they die. Populations reproduce faster, so generation time decreases with earlier maturity. In the populations we studied, the observation that the most productive adults were not the oldest and largest snails, but the snails which had been mature for only a few weeks, supports his hypothesis.

Growth rate is closely correlated with temperature (Dewitt 1954). The lack of obvious differences in growth rates of the two *P. heterostropha* populations was probably due to similar Moe Pond and Rat Cove summer temperatures. More distinct differences existed between cohorts. The first cohort (June to early August) at Moe Pond grew 4.5-5.5 mm in height in 3.5 to 4.5 weeks when temperatures were 19-23°C. The second

cohort (late August to October) grew 3.4 mm in height in 3.5 to 4.5 weeks when temperatures were 12–21°C. In July and August 1971, both sites had temperatures near 20°C, but the advanced maturity of the first cohort in both populations was reflected in their growth rate.

Height-weight coordinates and regression lines have steep slopes initially and level off slowly when the snails reached intermediate sizes. A regression line illustrating growth of *P. heterostropha* changes slope to the right when the snails reach 4 mm in height indicating that larger snails gain less weight per unit size increase than smaller gastropods. For example, when *P. heterostropha* grew from 0.8 mm to 2.3 mm it increased its weight 8-fold, from 2.8 to 4.3 mm its weight increased 3-fold, and from 5.8 mm to 7.3 mm its weight doubled.

Physa heterostropha populations were not obviously influenced by the chemical characteristics of the water that were measured. Data collected were within the ranges of Harman and Berg (1971) for central New York where these chemical parameters were considered to be unlimiting. Despite low density in winter (less than 1/m²), the populations increased to high densities in the spring because the fecundity of "the oldest and largest" snails remained high enough to compensate for winter mortality, which did not influence population density the following year. Physical stresses and predation caused this mortality. A small percentage (less than 1%) of overwintering adults did not succumb to these factors, but died because they reached the end of their life span.

Wave action has more effect on organisms living at Rat Cove than Moe Pond because the former is less protected from the wind. Snails were usually found concentrated in water 0 to 4 cm deep in the Rat Cove transect. Because snails (especially the young) are fragile and easily crushed by waves and dislodged rocks, it is important that they utilize the interstices between the stones in inhabiting a rocky lake shore (Clampitt 1970). They cling to the undersides of rocks for protection and were rarely observed grazing on the exposed areas. At

the Moe Pond transect, where the substrates are protected from severe wave action, snails were usually observed browsing on the upper surface of the cobbles. When those snails first hatched, they temporarily remained in water 0 to 3 cm in depth and later emigrated into water 4 to 10 cm deep. Adults were collected in June at depths from 0 to 10 cm until the first and second cohorts hatched. At that time adults in 0 to 3 cm of water moved into deeper areas.

The presence of ice affected the distribution of snails in both environments studied. In Moe Pond the transect area was frozen to the substrate in the winter and therefore uninhabitable. From January through April when ice covered Rat Cove, snails were observed dispersed in water from 3 to 30 cm. Cheatum (1934) noted that some snails migrate to deeper water during periods of ice cover, while others are often seen crawling on the underside of the ice. Plant production may be reduced in the winter because of reduced light transmission, but the snails are able to utilize the decayed plant materials accumulated in the fall (Clampitt 1970).

Fluctuating water levels at Rat Cove in June and July often exposed a strip of substrate 5 to 10 cm wide along the shore within short periods. Since egg masses required 1 to 2.5 weeks to develop, those oviposited in the shallowest areas were often exposed to the air. Many young snails were also exposed to the atmosphere and died.

One overriding factor is usually responsible for the control of a particular animal population. At any one time this factor may be food (Eisenberg 1966, Brockelman 1969); predation (Gillespie 1969, Murdoch 1971), density (Hariston *et al.* 1958, Murdoch 1971); adverse physical environment (Gillespie 1969); or life span (van Cleave 1934). In these populations, density correlated closely with predator population densities.

The leech *Helobdella stagnalis* and the flatworm *Dugesia tigrina* were the most abundant predators observed. Animals which are relatively prey-specific and are present year around, have a greater influence on snail populations than those predators which have a diverse diet and

are present only one or two months of the year (e.g., newts, dragonflies and predaceous diving beetles) (Baker 1918). The leech and flatworm populations in the study area fluctuated directly with the changes in snail population densities. This relationship was especially distinct when snails and leeches were at their highest and lowest population levels. The most abundant predators at Rat Cove in August and September correlated with the rapid reduction of *P. heterostropha*. The greatest numbers of leeches at Moe Pond also correlated with the reduction of *P. heterostropha* populations. The rapid decrease of snails and increase in leeches was obvious in Moe Pond in September and October. No *P. heterostropha* from the second cohort, larger than 3.5 mm in height, were collected in September and October. Presumably they were eaten by leeches. Populations of *D. tigrina* increased three to four weeks after *P. heterostropha* populations in Rat Cove reached peak densities. The average density of the leech population at Moe Pond was twice that of Rat Cove. This is consistent with the size of gastropod populations in Moe Pond, which averaged twice that of Rat Cove populations. Since leeches usually fluctuated directly with snail population density, or one to two weeks later, and the population of *D. tigrina* consistently increased three to four weeks after snail population density increased, it was apparent that these populations were acting in a density dependent manner.

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