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# POPULATION STUDIES OF FOUR SPECIES OF MOLLUSKS IN THE MADISON RIVER, YELLOWSTONE NATIONAL PARK

by

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VITA

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## ABSTRACT

Natural populations of Physa gyrina, Gyraulus deflectus, Valvata humeralis, and Pisidium compressum in a bed of aquatic macrophytes were sampled during the period April, 1964, through August, 1965. Population statistics for growth rate, rate of reproduction, mortality rate, rate of population change and production were calculated from analysis of field and laboratory data. Production was calculated graphically for selected cohorts by plotting population number versus mean individual biomass and determining the area under the curves. Production was also calculated by fitting data to a model population curve in the form:

$$\ln N_t = \ln N_o + d/g\ (\ln Q_o - \ln Q_t),$$

where $N_o$ and $N_t$ are population numbers at initial and later times of observation, $Q_o$ and $Q_t$ are mean individual biomass at initial and later times of observation, d is the mortality rate coefficient, and g is the growth rate coefficient. Net production ($P_n$) was then calculated by the equation:

$$P_n = N_o\ Q_o^{\ k}\ (1 - k)^{-1}\ (Q_t^{\ 1-k} - Q_o^{\ 1-k}),$$

where k is the constant, d/g, and other symbols are as explained above. Values of annual net production (shell-free dry weight per square meter) calculated from field data by the graphic method were as follows: Physa gyrina, 1.096 g/m$^2$; Gyraulus deflectus, 3.344 g/m$^2$; Valvata humeralis, 0.897 g/m$^2$; and Pisidium compressum, 3.018 g/m$^2$. Annual net production values calculated for model populations fitted to the data were as follows: Physa gyrina, 0.936 g/m$^2$; Gyraulus deflectus, 3.028 g/m$^2$; Valvata humeralis, 1.000 g/m$^2$; and Pisidium compressum, 2.611 g/m$^2$. The total net production calculated for model populations was 7.575 g/m$^2$, within ten percent of the value of 8.354 g/m$^2$ calculated graphically. Data showed a generally good fit to the model curve, and it was concluded that the model was adequate for calculating production of the species studied. The total annual net production of the three species of gastropods, which were the most important herbivorous invertebrates in the study area, was 5.150 g/m$^2$, equivalent to about 22,000 g cal/m$^2$. Assuming an efficiency (net production/assimilation) of 0.25, total gastropod assimilation was 88,000 g cal/m$^2$, equivalent to about 21.5 g/m$^2$ of plant material, which was approximately ten percent of the annual net primary production. Growth rates were affected by temperature and by age of individuals, but apparently were not limited by food supply. Most gastropods probably matured in one year, but Pisidium appeared to be partly biennial. Mortality rates were highest in spring and summer and lowest in winter. The principal causes of mortality appeared to be predation, which was temperature-correlated, and loss during high water, which was density-correlated. Reproductive periods of Physa, Gyraulus, and Pisidium extended from spring to fall, with maximum reproduction in July. Reproduction of Valvata was largely limited to the month of August.

# INTRODUCTION

Populations of four species of mollusks occurring in a bed of aquatic macrophytes were analyzed on the basis of samples taken over a 17 month period (April, 1964 to August 1965). From these samples and laboratory experiments, growth rate, birth rate, death rate, rate of population change, and production were estimated. The study of population statistics is an important approach to understanding the ecology of animal species, and the evaluation of such statistics may be much more informative than merely determining numbers or standing crop. Organ (1961) suggested that evolutionary trends and ecological relationships may be demonstrated by population statistics.

DeWitt (1954a, b; 1955) studied the ecology of *Physa gyrina* including reproduction, growth, life history, and intrinsic rate of natural increase. The investigations of Clampitt (1963), Heard (1963) and Thomas (1959, 1963) concerned population dynamics of species closely related to those considered here. Other studies of mollusk populations include those of Kohn (1959), Paine (1965), and Ritchie, *et al*. (1962). The contributions of Berg and Ockelmann (1959), Cheatum (1934), and Foster (1932) concern mollusks, but are less directly related to my investigation. Aquatic groups other than mollusks which have been studied with regard to their population dynamics include Cladocera (Hall, 1964; Slobodkin, 1954, 1959; Wright, 1965), Copepoda (Comita, 1964; Elster, 1954), Amphipoda (Cooper, 1965), Rotifera (Edmondson, 1945, 1946, 1960, 1965), Tricladida (Reynoldson, 1961), *Tipula* (Freeman, 1964), and fish (Allen, 1951; Gerking, 1962;

Ricker, 1946, 1954; Ricker and Foerster, 1948). Thorup (1963) studied growth and life-cycles of a variety of invertebrates. Extensive general reviews of the literature on population dynamics are found in Cole (1954), Slobodkin (1961), and Watt (1962).

The present investigation was confined to a section of the Madison River located 15.1 river kilometers east of the west boundary of Yellowstone National Park (Fig. 1). The Madison is formed by the confluence of

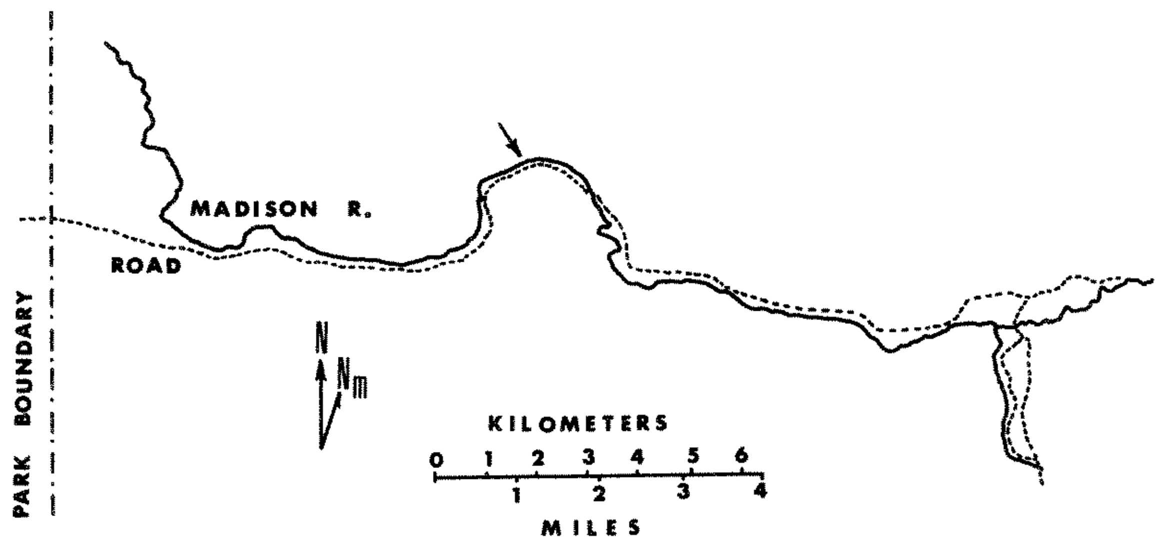


Figure 1. Madison River, Yellowstone National Park, showing study area (arrow).

the Firehole and Gibbon Rivers, both of which receive thermal water from geysers and hot springs. As a result, the temperature of the Madison River (Fig. 2) is higher than that of most Northern Rocky Mountain streams at a similar altitude (2046 meters msl). No ice was observed in the river

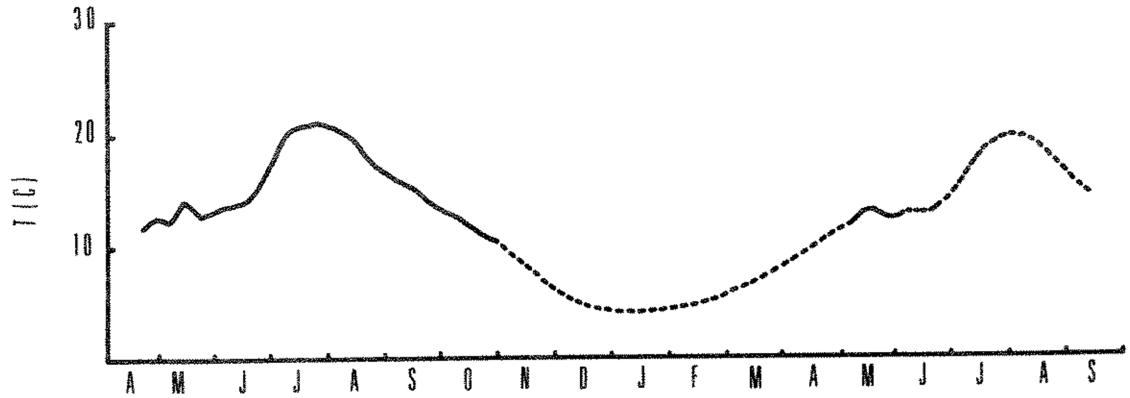


Figure 2. Average temperatures in Madison River April, 1964, to September, 1965. Solid line - thermograph data furnished by J. C. Wright. Dotted line estimated from maximum-minimum and pocket thermometer data.

at the study area during the period of the investigation. The water of the Madison River is high in dissolved solids and alkalinity, but low in divalent cations (Table 1). The most abundant cation is sodium. Abundant anions include chloride and sulfate. Silicate is high, but appears to be largely in undissociated form.

The study area was 150 meters long, and consisted of a channel about 15 meters wide by 2 meters deep flanked on each side by shallows which had a maximum depth of one meter and which were covered by a heavy growth of aquatic plants (Fig. 3). Surface current in late summer varied from approximately one meter per second in mid-channel to less than one centimeter per second in the vegetation beds. In late winter, when the plants had died down, surface current over the shallows increased to 15 - 20 centimeters per second, and increased to as high as 50 centimeters per

Table 1. Chemical analyses of water samples from the middle Madison River (Roeder, 1966).

| | Conductivity $K_{25} \times 10^6$ | Alkalinity meq/l | Calcium mwq/l | Magnesium meq/l | Potassium meq/l |
|---|---|---|---|---|---|
| Range | 274-488 | 1.25-2.50 | 0.09-0.21 | 0.00-0.10 | 0.12-0.28 |
| Mean | 424 | 2.13 | 0.14 | 0.04 | 0.28 |

| | Sodium meq/l | Chloride meq/l | Sulfate meq/l | Phosphate meq/l | Silicate meq/l | pH |
|---|---|---|---|---|---|---|
| Range | 2.10-4.80 | 0.89-1.83 | 0.41-0.46 | 0.006-0.017 | 2.02-2.65 | 7.30-7.89 |
| Mean | 3.82 | 1.58 | 0.44 | 0.013 | 2.42 | 7.60 |

second during the high water stage, which lasted from about May first to about July first in 1964 and to about July 20th in 1965. The area is separated from similar habitat above and below by broad shallow riffles. Qualitative samples were taken from the entire area, while quantitative samples were restricted to the shallows northwest of the channel. The bottom in these shallows consisted of silt and muck, while that of the channel was bedrock covered with a thin layer of sand and gravel.

*Potamogeton natans* was the most abundant plant in the study area. It occurred in nearly pure stands as did *P. foliosus* which covered less of the area. *Ranunculus aquatilus* grew sparsely in association with the above two species of *Potamogeton*, while *Chara* sp. was found in small patches throughout the area. Other macrophytes, found mainly in the shallow water along the shore, included *Hippurus vulgaris*, *Eleocharis* sp., *Sparganium* sp., *Myriophyllum exalbescens*, *Utricularia* sp., *Potamogeton filiformis*, and *Zannichellia palustris*. *Berula erecta* and an unidentified grass occurred in the riffles bordering the study area.

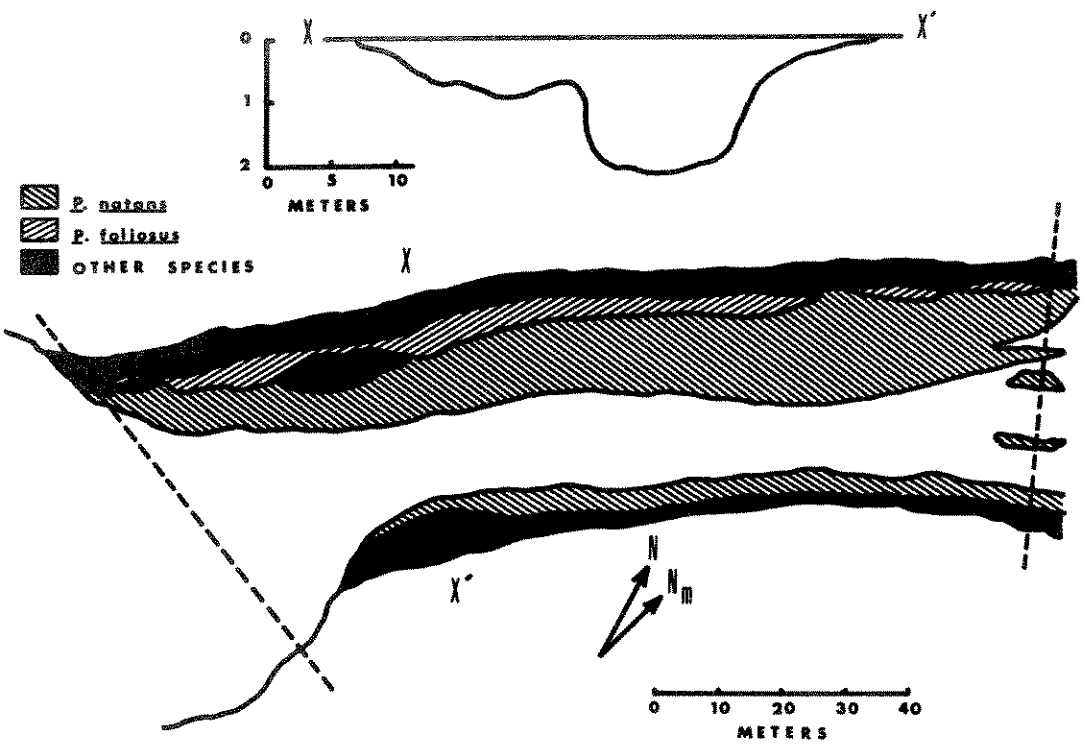


Figure 3. Madison River study area, showing cross-section through X - X', and distribution of plants.

Population studies included three gastropods — Gyraulus deflectus, Say, Physa gyrina, Say, and Valvata humeralis, Say; and one pelecypod — Pisidium compressum, Prime. All four were primarily in beds of aquatic macrophytes. A few Pisidium casertanum were mixed with the population of P. compressum, but in general were restricted to the riffles.

In addition to the mollusks considered in this study, abundant macro-invertebrates collected were Tanytarsus sp., Donacia hirticollis, Agrion aequabile, Simulium sp. and Helisoma trivolvis binneyi. Leptocella sp.

was numerous during the spring and summer of 1963, but was not taken after the winter of 1964. *Gammarus* sp. was generally uncommon but occasionally appeared in fairly large numbers. Hirudinea and Oligochaeta were found in most collections, and the latter were sometimes numerous. An unidentified aphid was abundant on the floating leaves of *Potamogeton natans* in August and September of 1963, and again in September and October of 1965. *Margaritana margaritifera* and *Helicopsyche* sp. were occasionally collected.

*Salmo gairdneri*, *Rhinichthys cataractae*, and *Cottus bairdi* were taken in the study area. Other fishes common in the Madison River were *Salmo trutta*, *Prosopium williamsoni*, *Catostomus catostomus*, *Pantosteus platyrhynchus*, and *Gila atraria*. Muskrats and several species of waterfowl also frequented the study area.

## METHODS

Organisms were collected with a mechanical sampler (Gillespie and Brown, 1966), consisting of a 0.1 square meter frame with an attached net and a gear-driven closing mechanism. Mesh size in the nylon net averaged 0.8 x 0.7 mm, which permitted significant losses of newly hatched individuals of some species. Correction factors, based on losses observed in laboratory tests, were applied when necessary. Collections for each date were taken along transects, with each transect located upstream from those taken previously to avoid sampling disturbed areas. Sites of individual samples were chosen at random distances from shore in each transect, but only sites which fell within beds of *Potamogeton natans* or *P. foliosus* were used.

After each sample was removed from the sampler, it was placed in a plastic bag and preserved in 5 percent formalin. Samples were taken to the laboratory and rinsed free of formalin. All macroinvertebrates were separated from plant material and detritus, sorted by species, and preserved in 70 percent ethanol. The species used in the population study were then sorted into four size classes, designated I, II, III, and IV, from smallest to largest, and counted. Fingernail clams were sized by sorting on a grid under a microscope, while snails were washed through a series of graded screens. Adult fingernail clams were dissected and embryos counted. All mollusks were decalcified with 0.5 N HCl, dried to constant weight at 65 degrees C, and weighed on a Mettler balance. The small error introduced by this procedure was ignored (Richards and Richards, 1965). Part of the routine laboratory work was performed by paid assistants.

Population number per square meter (N), population biomass (W, $mg/m^2$) and mean individual biomass (Q, mg) were estimated from collection data. Migration into the study area was assumed to be negligible, and losses to emigration or downstream drift were treated as mortality. Population statistics for rate of population change, birth rate, and mortality rate were calculated by the equation:

$$r = b - d = dN/Ndt, \qquad (1)$$

where r, b, and d are, respectively, coefficients of rate of population change, birth rate, and mortality rate; N is the population, and t is time in days (Edmondson, 1960). In integral form:

$$N_t = N_o e^{rt}, \tag{2}$$

or:

$$N_t = N_o e^{(b - d)t}, \tag{3}$$

where e is the base of natural logarithms, $N_t$ is the population at the time of collection, and $N_o$ is the population at the previous collection. Taking the natural logarithms of both sides of equation 3, and rearranging:

$$b - d = (\ln N_t - \ln N_o)/t \tag{4}$$

The populations of gastropods, in which reproduction was largely restricted to a short period in summer, were treated as cohorts of uniform age. To avoid errors caused by including adults surviving from the previous generation and immature individuals hatched "out of season", calculations were restricted to the dominant annual generation which was followed through the year by size-frequency analyses of all collections. This method of interpreting population data is necessarily subject to the judgement of the investigator, especially with regard to selection of size classes used in estimating the population, and it is possible to obtain more than one interpretation of a set of data. Nevertheless, it was felt that this approach gave a more realistic picture of population dynamics than trying to interpret data for the total population. Average values of d were determined by fitting a survivorship curve to the population data by the method of least squares. Summer values for d were assumed to continue through the reproductive period, and the coefficient of birth rate was calculated by:

$$b = r + d. \tag{5}$$

The population of Pisidium compressum was not treated as a cohort, since a significant amount of reproduction occurred during much of the year. Because this species is hermaphroditic and ovoviviparous, the finite birth rate (B) could be determined by dissecting the adults, counting the embryos, and determining the average number of embryos per individual (E). Then:

$$B = E/t', \tag{6}$$

where t' is the time of development, in days, of the embryos from the size of the smallest counted to birth (equivalent to "D" of Edmondson, 1960; and Wright, 1965), and B is expressed as births per individual per day (Edmondson, 1960). Only embryos of 0.52 mm length or greater were counted, since smaller individuals were not easily located by gross dissection. The coefficient of instantaneous birth rate was calculated by:

$$b = \ln (B + 1), \tag{7}$$

and r was determined from population data. Then:

$$d = b - r. \tag{8}$$

Total reproduction (B') over a period of time was calculated by:

$$B' = \sum_{x=1}^{y} \overline{N}_x B_x t_x, \tag{9}$$

where $\overline{N}_x$ is the mean population during each time interval, $B_x$ is the finite rate of reproduction for each interval, $t_x$ is the time in days of each interval, and y is the number of intervals in the total period.

Growth was estimated from data on field populations and from measurements of captive individuals. Instantaneous growth rate was computed as:

$$dQ/dt = gQ, \tag{10}$$

where Q is the mean shell-free dry weight of individuals, g is the coefficient of growth rate, and t is time in days. Calculations were made from the form:

$$g = (\ln Q_t - \ln Q_o)/t, \tag{11}$$

where $Q_t$ is mean individual weight at time of an observation, and $Q_o$ is mean individual weight at the time of a previous observation. An average value of g was obtained for each species by fitting a curve to the data. Total net production ($P_n$) was estimated by the method used by Allen (1951) and by Neess and Dugdale (1959). For a uniform age cohort, total net production equals the area under a graph of number versus mean individual weight, or growth-survivorship curve. This is expressed by:

$$P_n = \int_{Q_o}^{Q_t} N dQ. \tag{12}$$

Determinations of $P_n$ were obtained by constructing graphs, and obtaining the area with a polar planimeter. Data were also fitted to the population model proposed by Neess and Dugdale (1959), using the equation:

$$\ln N_t = \ln N_o + {}^{d}/_{g} (\ln Q_o - \ln Q_t). \tag{13}$$

Since N is given as a function of Q, production is obtained by integration of equation 12:

$$P_n = N_o Q_o^{\,k} (1 - k)^{-1} (Q_{ta}^{\,1 - k} - Q_o^{\,1 - k}), \tag{14}$$

where k is the constant, ${}^{d}/_{g}$, and $Q_{ta}$ is the final value of $Q_t$ for adult animals.

The above method of obtaining $P_n$ was applied directly to the populations of gastropods, which were treated as cohorts. For the fingernail clams, a modification of the method was used. Estimates of the growth-survivorship curve were obtained by following a size class of individuals through their life cycles, and by use of an average size-frequency curve. A calculated value of net production ($P_c$) was obtained from these curves, and divided by $N_o$, the estimated number at birth (obtained by extrapolation) in the growth-survivorship curve. The production per individual born into the population was computed as:

$$P_i = P_c/N_o = 1/N_o \int_{Q_o}^{Q_t} N dQ. \qquad (15)$$

The net production of the population over a given period of time was obtained by:

$$P_n = B' P_i, \qquad (16)$$

where B' is the total number of births in the population during the given time, calculated by equation 9.

## RESULTS

Physa gyrina. Examination of population data for this species (Table 2) showed a spring low followed by a rapid increase to a peak in August. Maximum biomass (W) of the 1964-1965 generation occurred in September, and minimum biomass in June. The increase in numbers was accompanied by a shift in population structure in 1964 from 82.5 percent adults to 85.7 percent juveniles (Fig. 4, A). Those individuals hatched after July 7th, and before August 6th, made up an estimated 78 percent of the 1964 generation, and an attempt was made to follow the life-history of this group

Table 2. Population data for Physa gyrina.

| Date | N ± SE | W | r | b | d |
|---|---|---|---|---|---|
| 5/ 5/64 | 894 ± 100.5 | 791.0 | -0.0292 | 0.00 | 0.0292 |
| 6/28/64 | 185 ± 69.9 | 213.5 | 0.0548 | 0.0745 | 0.0197 |
| 7/ 7/64 | 303 ± 74.4 | 593.6 | 0.0394 | 0.0591 | 0.0197 |
| 7/21/64 | 526 ± 77.3 | 496.3 | 0.0812 | 0.1009 | 0.0197 |
| 8/ 6/64 | 1928 ± 833.7 | 654.0 | -0.0107 | 0.0090 | 0.0197 |
| 9/12/64 | 1296 ± 377.4 | 724.3 | -0.0197 | 0.00 | 0.0197 |
| 10/ 9/64 | 762 ± 307.9 | 473.3 | -0.0041 | 0.0001 | 0.0042 |
| 2/ 7/65 | 466 ± 238.1 | 213.7 | -0.0132 | -0.0090 | 0.0042 |
| 4/25/65 | 168 ± 64.0 | 205.4 | 0.0056 | 0.0098 | 0.0042 |
| 7/ 9/65 | 255 ± 34.6 | 157.6 | 0.0613 | 0.0810 | 0.0197 |
| 8/16/65 | 2460 ± 309.1 | 1372.8 | ------ | ------ | ------ |

by size-frequency analyses, using four size classes with mean weights of 0.0916 mg, 0.3081 mg, 0.9220 mg, and 2.5637 mg. Population and weight estimates were used to calculate mortality and growth rates (Table 3).

The survivorship curve obtained (Fig. 5) was fitted to equation 4, with b considered equal to zero, and average mortality rate coefficient (d) determined from the slope. Best fit was obtained by dividing the curve into two parts with mortality rate coefficients of 0.0197 in late summer and fall, and 0.0042 in winter and spring. The high estimate of N for August, 1965, may result from a sampling error, but is included in the above mortality rates. If this August estimate is correct, the population may have been concentrated in the Potamogeton beds during breeding season, and later dispersed to other habitat. The high apparent mortality in the fall may have resulted from dispersal out of the study area. The coefficient of reproductive rate (b) was determined for intervals between samples by equation 5, using the average values of d for each time of year (Table 2). The

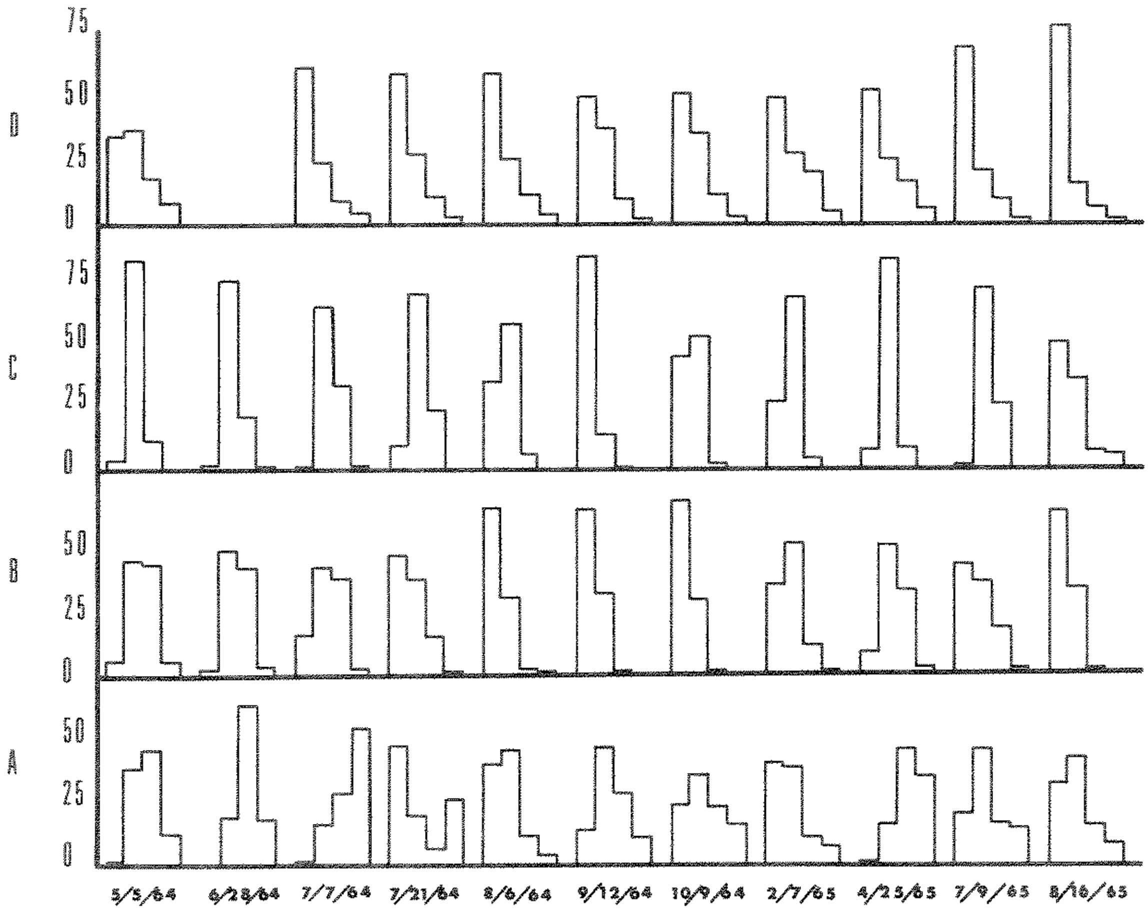


Figure 4. Frequency (percent) histograms for Physa gyrina (A), Gyraulus deflectus (B), Valvata humeralis (C), and Pisidium compressum (D). Each histogram represents four size groups - smallest at left and progressively larger to right.

maximum observed value of b was 0.1009 (7/21/64 - 8/6/64), which corresponds to a finite hatching rate of 0.1062 individuals per individual per day (Equation 7). The total number of individuals introduced into the population (B') during 1964 was 3133.

Table 3. Population data for a selected population of Physa gyrina.

| Date | N | d | Q | g |
|---|---|---|---|---|
| 7/21/64 | 250 | ------ | 0.094 | 0.0453 |
| 8/ 6/64 | 1650 | 0.0269 | 0.194 | 0.0128 |
| 9/12/64 | 610 | 0.0112 | 0.312 | 0.0132 |
| 10/ 9/64 | 451 | 0.0135 | 0.446 | 0.0140 |
| 2/ 7/65 | 88 | 0.0050 | 1.575 | 0.0043 |
| 4/25/65 | 60 | 0.0061 | 2.196 | 0.0002 |
| 7/ 9/65 | 38 | -0.0462 | 2.220 | 0.0067 |
| 8/16/65 | 220 | ------ | 2.860 | ------ |

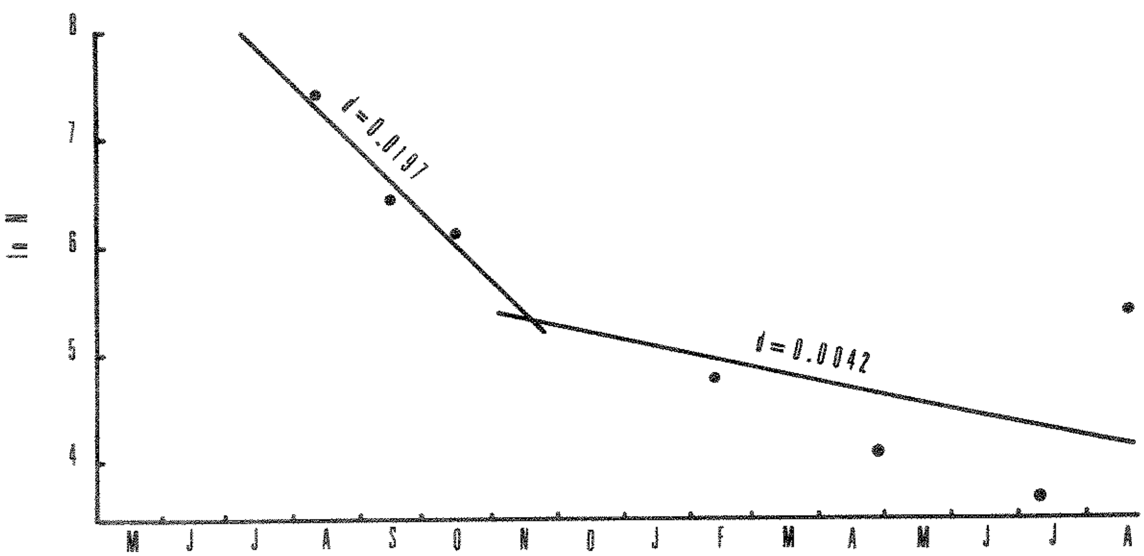


Figure 5. Mortality curves for a selected population of Physa gyrina, May, 1964, through August, 1965.

A growth curve (Fig. 6) was constructed from the mean weight data,

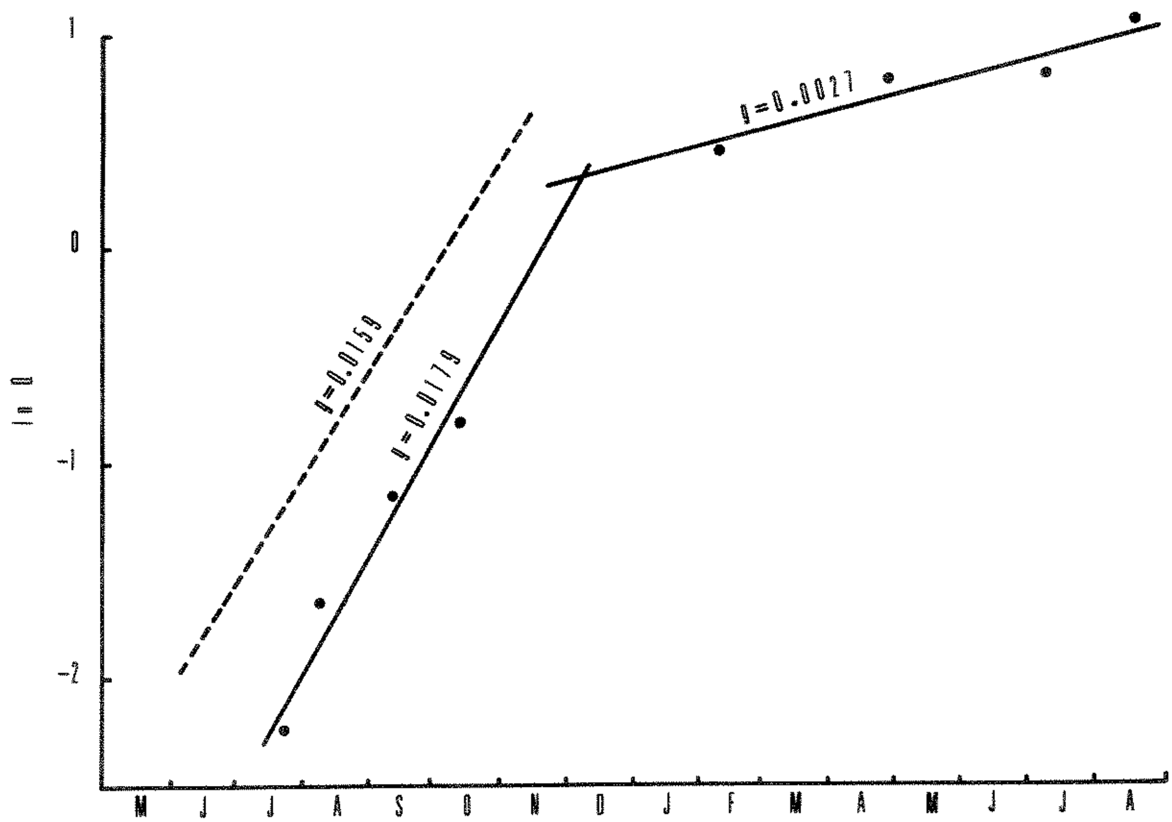


Figure 6. Growth curves for Physa gyrina, May, 1964, through August, 1965. Aquarium population - broken line; field population - solid line.

fitted to equation 10, and growth rate coefficient (g) determined from the slope. Growth rate is expected to vary with temperature and other factors, but a reasonably good fit was obtained by breaking the data into two sections corresponding with the two parts of the survivorship curve. This gave values for g of 0.0179 in summer and fall and 0.0027 in winter and spring. Growth rate coefficient of individuals raised in aquaria at a mean temperature of 19.5 C averaged 0.0159. DeWitt's (1954a) data yield a much higher value (g = 0.136) than any of the above, but this is only an approximation, since this growth data were converted from shell length to shell-free dry weight for comparison with my results.

Survivorship and growth data were combined (Fig. 7) and fitted to

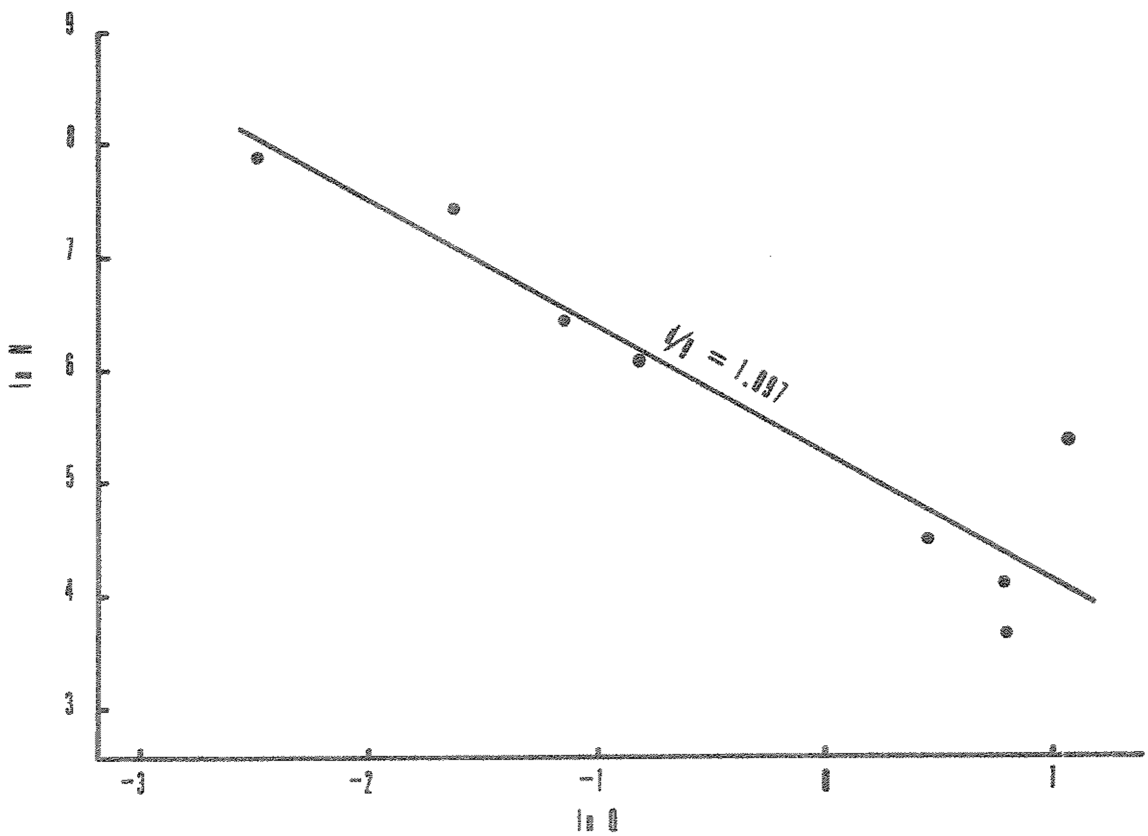


Figure 7. Growth-mortality curve for a selected population of Physa gyrina.

Neess and Dugdale's (1959) model (Equation 13). The average value of d/g obtained by the method of least squares was 1.097, with $N_o$ estimated at 2754. Ratios of d/g determined for the two sections of the survivorship and growth curves were 1.103 for summer and fall and 1.556 for winter and spring (average 1.405).

Net production was obtained from the field data by planimetry and from the smoothed curve by equation 14. Using estimated values of $Q_o$ = 0.09 mg, and $N_o$ = 2430, net production was calculated from field data at 854.50 mg/m$^2$. The value obtained by equation 14 was 730.07 mg/m$^2$ ($N_o$ = 2754, $Q_o$ = 0.09, d/g = 1.097). Since these values were for an estimated 78 percent of the 1964 generation, the values were adjusted, assuming that production of individuals hatched at other times of year was equivalent to that of the group studied. Total net production for the 1964 - 1965 generation was calculated to be 1095.51 mg/m$^2$ from field data, and 935.99 mg/m$^2$ from a model population fitted to the data.

Gyraulus deflectus. Field data for this species (Table 4) show a low population in early summer of 1964, followed by a rather slow increase to a peak in October. Maximum biomass (W) was reached in June of 1964, and in April of 1965. Population peaks are accompanied by a changing population structure as with Physa (Fig. 4, B). An attempt was made to follow a generation through a lifecycle by size-frequency analysis, using four size classes with mean weights of 0.0682 mg, 0.2064 mg, 0.401 mg, and 0.568 mg, but meaningful data were derived only from the winter and spring samples. Data from summer collections were difficult to interpret because the 1964 reproductive season extended from early July to October, with no definite

Table 4. Population data for *Gyraulus deflectus*.

| Date | N ± SE | W | r | b | d |
|---|---|---|---|---|---|
| 5/ 5/64 | 2686 ± 250.9 | 802.0 | 0.0046 | 0.0283 | 0.0237 |
| 6/28/64 | 3436 ± 1082.0 | 1021.7 | -0.0089 | 0.0234 | 0.0323 |
| 7/ 7/64 | 3173 ± 471.6 | 856.4 | 0.0342 | 0.0665 | 0.0323 |
| 7/21/64 | 5122 ± 1803.8 | 850.7 | 0.0028 | 0.0351 | 0.0323 |
| 8/ 6/64 | 5357 ± 1115.6 | 492.2 | 0.0054 | 0.0377 | 0.0323 |
| 9/12/64 | 6010 ± 1531.6 | 396.2 | 0.0084 | 0.0407 | 0.0323 |
| 10/ 9/64 | 7548 ± 515.8 | 570.2 | -0.0002 | 0.0000 | 0.0002 |
| 2/ 7/65 | 7381 ± 738.4 | 1299.7 | -0.0053 | 0.0000 | 0.0053 |
| 4/25/65 | 4926 ± 870.4 | 1342.3 | -0.0031 | 0.0206 | 0.0237 |
| 7/ 9/65 | 3902 ± 599.8 | 689.7 | 0.0361 | 0.0684 | 0.0323 |
| 8/16/65 | 15,378 ± 3663.0 | 1329.1 | ------ | ------ | ------ |

population peak. Another difficulty was that newly hatched animals were able to pass through the net used, so that during periods of peak reproduction, population estimates were much lower than the true population. Data in Table 4 are uncorrected, but a correction factor was applied to data used to calculate population statistics (Table 5), assuming a loss of 40 percent of class I individuals during reproductive periods. Calculations included an estimated 81 percent of the 1964 - 1965 generation.

The survivorship curve (Fig. 8) was fitted to equation 4 with b considered equal to zero, yielding average mortality rate coefficients (d) of 0.0048 for the winter months and 0.0323 for spring and early summer. Mortality of a small group of *Gyraulus* was estimated for a single month (8/6/64 - 9/12/64) during the summer, and d was found to equal 0.0274. This value is probably an underestimate, since recruitment of young animals to the population could not be completely accounted for. The reproductive rate coefficient (b) was calculated by equation 5, assuming

Table 5. Population data for a selected population of *Gyraulus deflectus*.

| Date | N | d | Q | g |
|---|---|---|---|---|
| 10/ 9/64 | 11,500* | 0.0037 | 0.073 | 0.0072 |
| 2/ 7/65 | 7,343 | 0.0068 | 0.174 | 0.0061 |
| 4/25/65 | 4,374 | 0.0237 | 0.278 | 0.0051 |
| 7/ 9/65 | 736 | 0.0533 | 0.408 | 0.0079 |
| 8/16/65 | 97 | ------ | 0.551 | ------ |

* Corrected for losses through net.

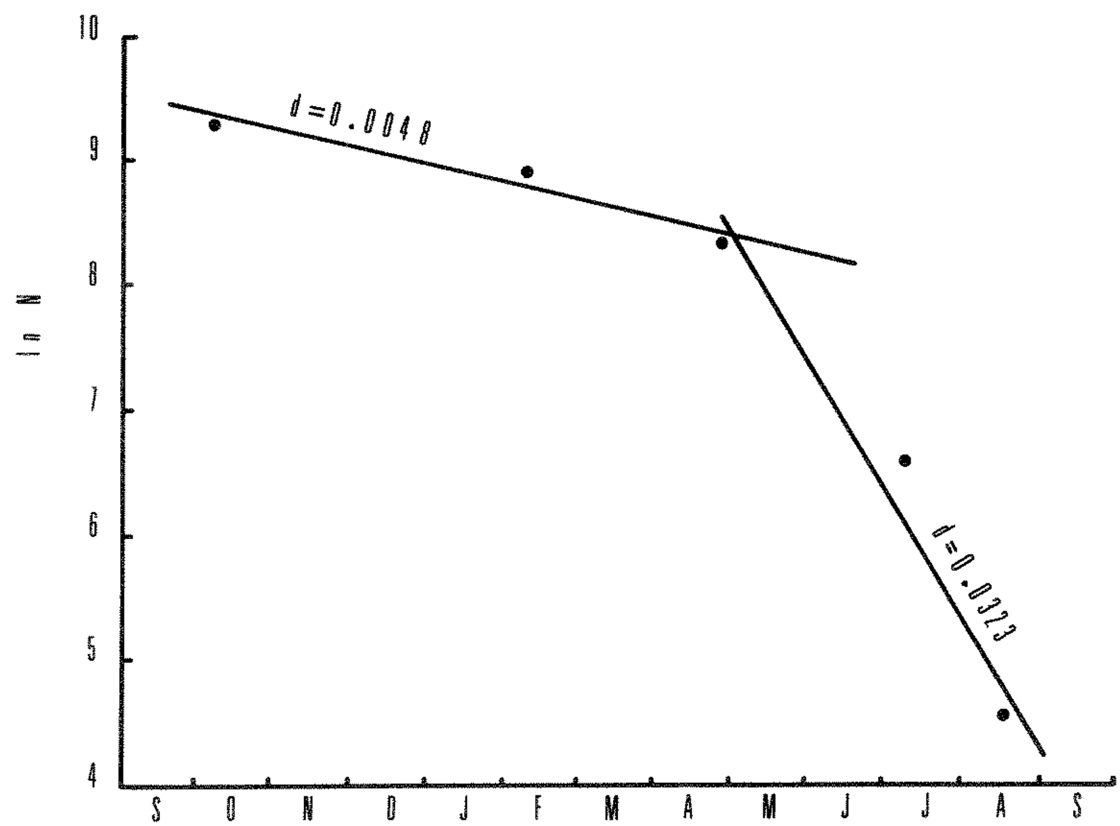


Figure 8. Mortality curves for a selected population of *Gyraulus deflectus*, September, 1964, through September, 1965.

that d was equal to 0.0323 during the reproductive season (Table 4). Reproduction was assumed to be zero during the winter. Total reproduction (B') was calculated to be 28,315 by equation 9.

The growth curve (Fig. 9) yielded an average growth rate coefficient

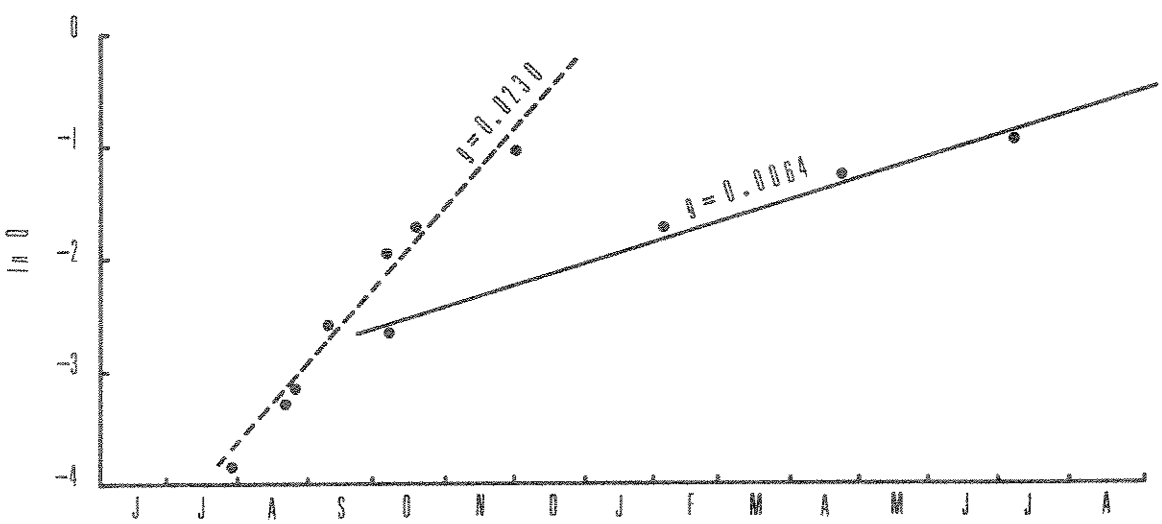


Figure 9. Growth curves for Gyraulus deflectus, June, 1964, through August, 1965. Aquarium population - broken line; field population - solid line.

(g) of 0.0064 when fitted to equation 10, with no increase in spring. Data for the total population yielded almost identical growth rate (g = 0.0065) for the winter months (10/9/64 - 4/25/65). An approximate summer growth rate coefficient of 0.0230 was determined from a group of animals raised in aquaria at a mean temperature of 19.5 C.

Data for growth and survivorship were combined (Fig. 10) and fitted to

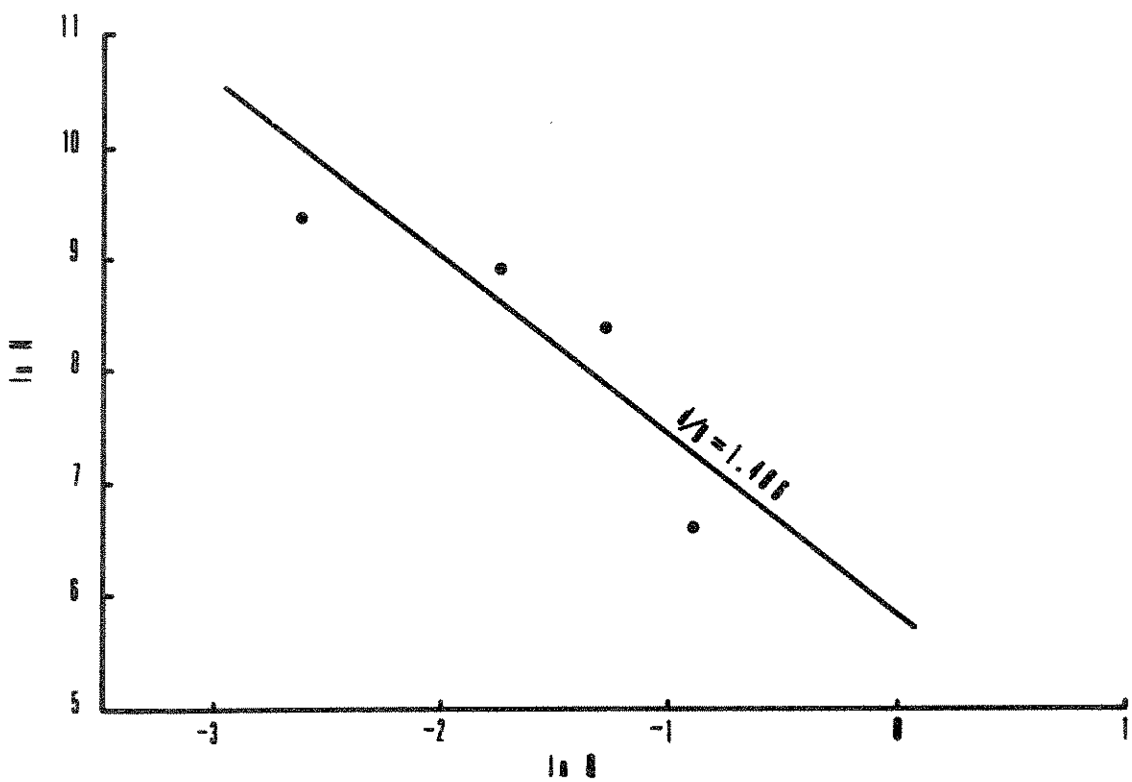


Figure 10. Growth-mortality curve for a selected population of Gyraulus deflectus.

equation 13, even though data were inadequate for fitting the entire curve. The calculated average value of d/g was 1.406. Assuming a constant value of d/g, and an average summer growth rate coefficient of 0.0230, an average summer value for d of 0.0323 was obtained, which is identical to the spring and early summer value obtained above.

Net production, which was calculated from field data by planimetry using estimated values of $Q_o$ = 0.037 mg and $N_o$ = 22,935, was 2708.25 mg/$m^2$.

The value of $P_n$ calculated by equation 14, with $Q_o = 0.037$ mg, $N_o$ = 40,120, and d/g = 1.406, was 2453.06 mg/m$^2$. Since these values were for an estimated 81 percent of the 1964 - 1965 generation, total net production calculated from field data was 3343.52 mg/m$^2$, and the value calculated for a model population fitted to the data was 3028.47 mg/m$^2$.

*Valvata humeralis*. Data for this species (Table 6) shows a population

Table 6. Population data for *Valvata humeralis*.

| Date | N ± SE | W | r | b | d |
|---|---|---|---|---|---|
| 5/ 5/64 | 7686 ± 799.4 | 2670.6 | -0.0202 | 0.0 | 0.0202 |
| 6/28/64 | 2583 ± 666.1 | 921.9 | -0.1196 | 0.0 | 0.1196 |
| 7/ 7/64 | 880 ± 204.6 | 328.6 | -0.1022 | 0.0 | 0.1022 |
| 7/21/64 | 210 ± 72.9 | 74.2 | -0.0589 | 0.0 | 0.0589 |
| 8/ 6/64 | 82 ± 29.0 | 20.0 | 0.0948 | 0.1194 | 0.0246 |
| 9/12/64 | 2738 ± 699.0 | 271.2 | -0.0026 | 0.0 | 0.0026 |
| 10/ 9/64 | 2553 ± 482.3 | 563.4 | -0.0078 | 0.0 | 0.0078 |
| 2/ 7/65 | 997 ± 118.7 | 275.0 | 0.0007 | 0.0 | -0.0007 |
| 4/25/65 | 1052 ± 174.0 | 345.7 | -0.0141 | 0.0 | 0.0141 |
| 7/ 9/65 | 366 ± 65.7 | 132.3 | -0.0319 | 0.0185 | 0.0504 |
| 8/16/65 | 109 ± 23.7 | 24.2 | ------ | ------ | ------ |

minimum in August, 1964, and an abrupt recovery to a peak in September. The September population did not reach the level of the previous May, and was far below the presumed level of the previous autumn. Size-frequency analyses were based on four size classes with mean weights of 0.0941 mg, 0.3275 mg, 0.4815 mg, and 0.5375 mg (Fig. 4, C). Calculation of population statistics could be based on the entire population because the change from old to new generation was so nearly complete, and the reproductive period so short. Most of the 1963 - 1964 generation apparently died before the 1964 - 1965 generation hatched. Newly hatched individuals could pass through the collection net, and data used in calculations (Table 7) were corrected, assuming a 40 percent loss of class I individuals during the reproductive period. Calculations were assumed to include the entire 1964 - 1965 generation.

Table 7. Population data for a selected population of Valvata humeralis.

| Date | N | d | Q | g |
|---|---|---|---|---|
| 9/12/64 | 4317* | 0.0173 | 0.087 | 0.0333 |
| 10/ 9/64 | 2709 | 0.0083 | 0.215 | 0.0021 |
| 2/ 7/65 | 997 | -0.0007 | 0.276 | 0.0023 |
| 4/25/65 | 1052 | 0.0141 | 0.329 | 0.0013 |
| 7/ 9/65 | 366 | 0.0504 | 0.362 | 0.0013 |
| 8/16/65 | 54 | ------ | 0.380 | ------ |

* Corrected for losses through net.

The survivorship curve (Fig. 11), fitted to equation 4, yielded average mortality rate coefficients (d) of 0.0173 in autumn, 0.0051 in winter, and 0.0246 in spring and summer. High summer mortality apparently is a result of adults dying after reproduction. A survivorship curve could be fitted for the entire period (9/12/64 - 7/9/65), with an average value for d of 0.0073. The coefficient of reproductive rate (b) for the reproductive period was determined from equation 5, using the average value of d for the 4/25/65 - 8/16/65 period (0.0246). This yields a value for b of 0.1199, which is equivalent to a finite birth rate (B) of 0.132, and total reproduction (B') of 6886 individuals/$m^2$.

The growth curve (Fig. 12) showed rapid growth (g = 0.0333) during autumn (September - October), and very slow growth (g = 0.0018) during the rest of the year. No increase in growth rate of adults was observed in

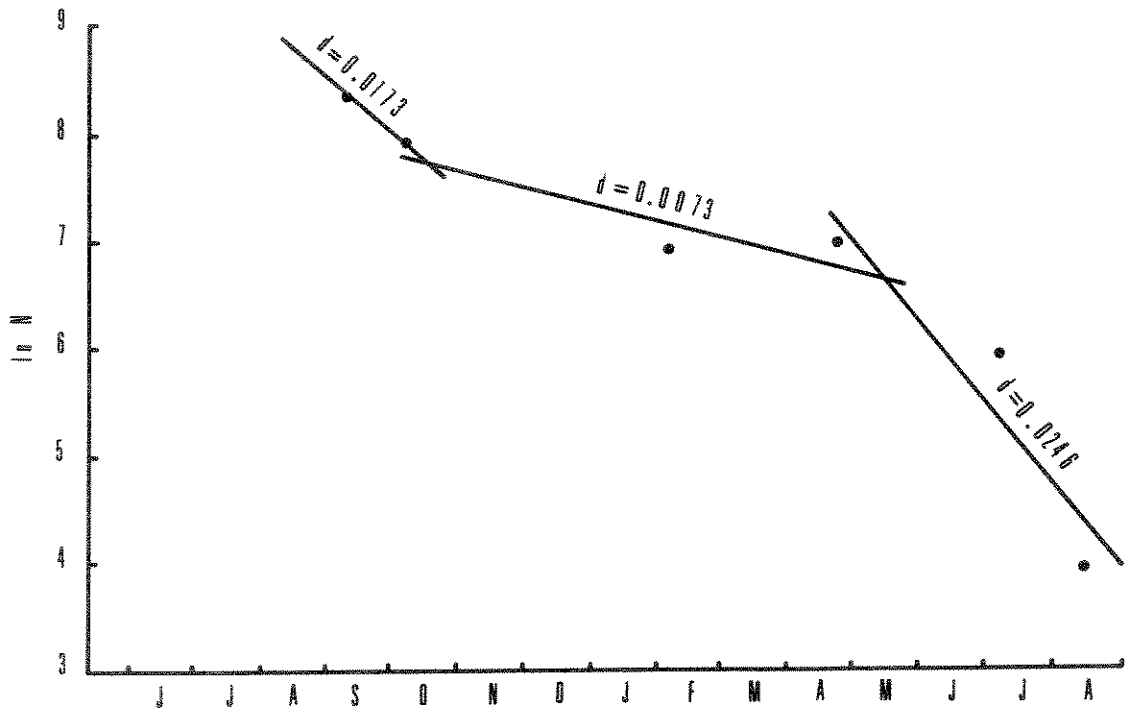


Figure 11. Mortality curves for a selected population of Valvata humeralis, June, 1964, through August, 1965.

spring and summer. The growth rate coefficient was 0.0550 for individuals raised in aquaria at a mean temperature of 19.5 C.

The growth-survivorship curve (Fig. 13) was fitted to equation 13, yielding a calculated average value for d/g of 1.461. The average mortality rate coefficient was calculated to be 0.0486, assuming a constant ratio d/g and an average growth rate coefficient of 0.0333 during the reproductive period. This value for d is considerably higher than the value used above, and would give a correspondingly higher birth rate for the reproductive period (b = 0.1434).

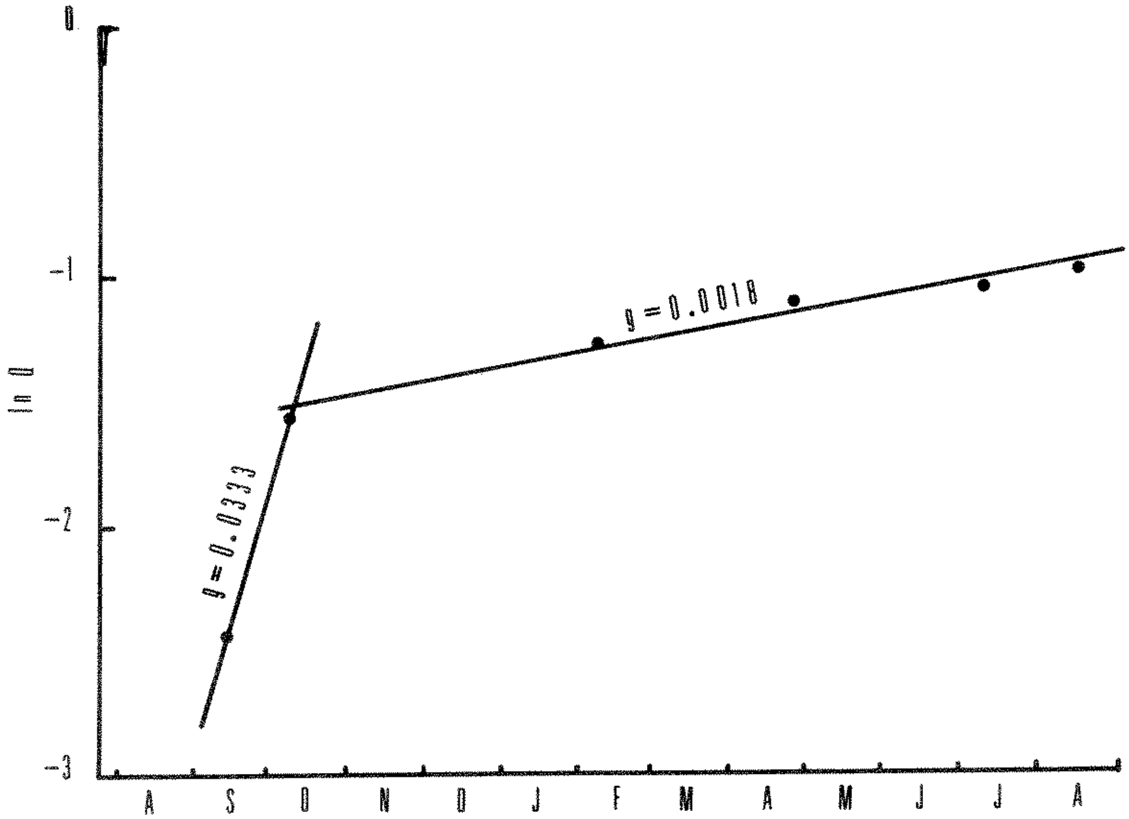


Figure 12. Growth curves for a population of Valvata humeralis, August, 1964, through August, 1965.

Net production, calculated by planimetry from field data, using estimated values of $Q_o = 0.041$ mg, and $N_o = 6886$, was 897.00 mg/m$^2$. Net production was 999.61 mg/m$^2$ for a model population fitted to the data, calculated by equation 14, using estimated values of $Q_o = 0.041$, $N_o = 16{,}564$, and $d/g = 1.461$.

Pisidium compressum. The population of Pisidium was made up almost entirely of P. compressum, and was treated as a single species population. Al-

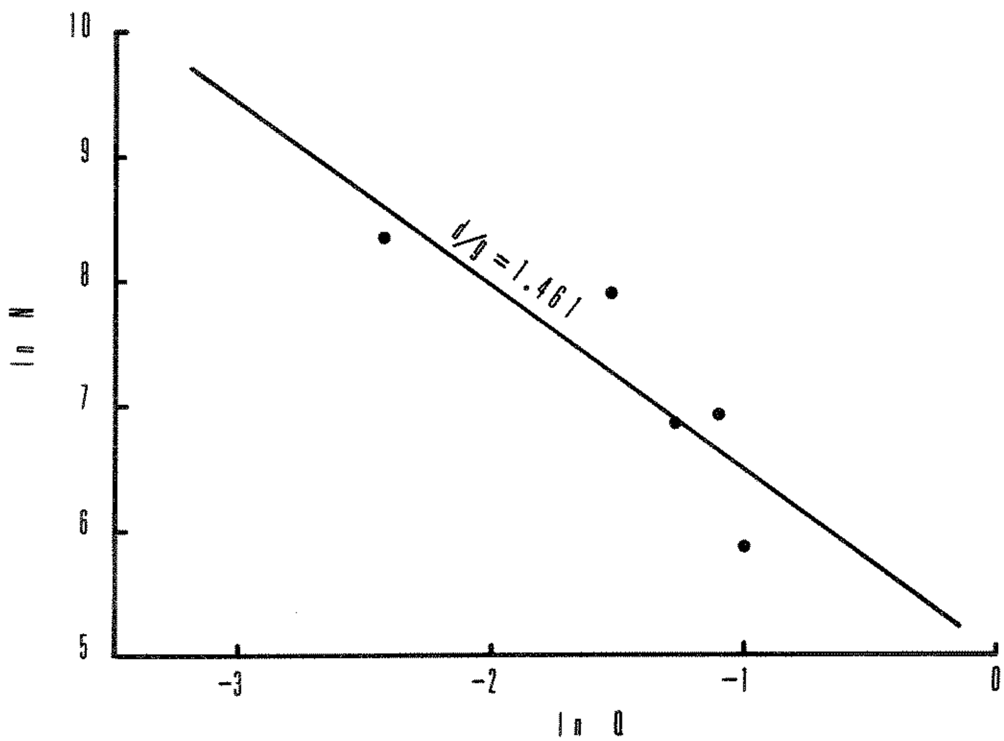


Figure 13. Growth-mortality curve for a selected population of *Valvata humeralis*.

though some *P. casertanum* were included in the population, these were considered to be too few to have any significant effect on calculations. The population minimum occurred in July and the maximum in October, 1964 (Table 8). In 1965, the population minimum was in July and the maximum in August. However, since no data were collected after August, further increases may have occurred. Maximum biomass was reached in late April or early May, just prior to the high water stage of the river, and minimum

Table 8. Population data for Pisidium compressum.

| Date | N ± SE | W | r | b | d |
|---|---|---|---|---|---|
| 5/ 5/64 | 5138 ± 369.4 | 1269.8 | -0.0183 | 0.0073 | 0.0256 |
| 7/ 7/64 | 1620 ± 428.9 | 263.8 | 0.0079 | 0.0375 | 0.0296 |
| 7/21/64 | 1810 ± 514.4 | 267.6 | 0.0279 | 0.0124 | -0.0155 |
| 8/ 6/64 | 2829 ± 500.2 | 450.7 | 0.0189 | 0.0225 | 0.0036 |
| 9/12/64 | 5688 ± 2280.5 | 780.4 | 0.0006 | 0.0073 | 0.0067 |
| 10/ 9/64 | 5781 ± 1322.6 | 753.6 | -0.0015 | 0.0003 | 0.0018 |
| 2/ 7/65 | 4833 ± 1533.5 | 910.4 | -0.0014 | 0.0000 | 0.0014 |
| 4/25/65 | 4334 ± 624.3 | 952.4 | -0.0114 | 0.0015 | 0.0129 |
| 7/ 9/65 | 1837 ± 400.8 | 258.8 | 0.0313 | 0.0121 | -0.0193 |
| 8/16/65 | 6040 ± 1004.4 | 706.2 | ----- | 0.0530 | ----- |

biomass occurred just after high water. The distribution of Pisidium was very uneven during the high water period, and the animals were frequently swept into piles in sheltered areas by the swift current. For this reason sampling was not adequate for the June, 1964, collection, and data from this collection were not used.

Population data were used to calculate coefficients of rates of population change (r) for each sampling period (Table 8; Fig. 14) by equation 2. Coefficients of reproductive rates (b) were calculated by equation 7 from finite birth rates (B), which were obtained by equation 6. Development time (t') was difficult to determine accurately, since growing embryos could not be observed inside the adults. Development time was estimated at 11.5 days from size-frequency analysis of embryos collected in late June and early July of 1964, and this value was used in calculating B for summer collections (July - September). An estimated value of t' = 16 days was used to calculate B for spring and fall collections. The total number of individuals born into the population (B') during 1964 was

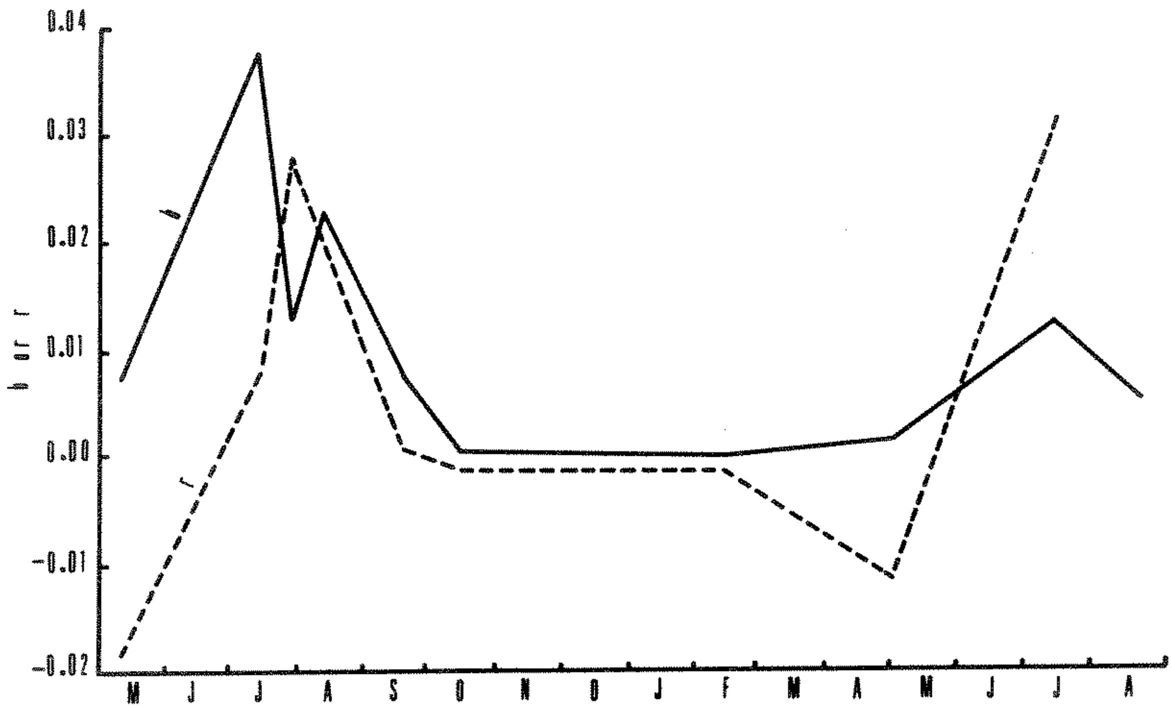


Figure 14. Coefficients of reproduction rate (solid line) and rate of population change (broken line) for Pisidium compressum, May, 1964, through August, 1965.

9569, as estimated by equation 17.

The reproductive period for this species extended from late April to October, with maximum reproduction occurring in early July. Only one collection (2/7/65) contained no embryos. As a result of the long period of reproduction, the smallest size class (I) was the most numerous in all but one collection (Fig. 4, D). Average weights of the four size classes were 0.0710 mg, 0.1691 mg, 0.4441 mg, and 0.8429 mg.

The mortality rate coefficient (d) was calculated by equation 8 (Table

8, Fig. 15). On two collection dates (7/21/64 and 7/9/65) a negative

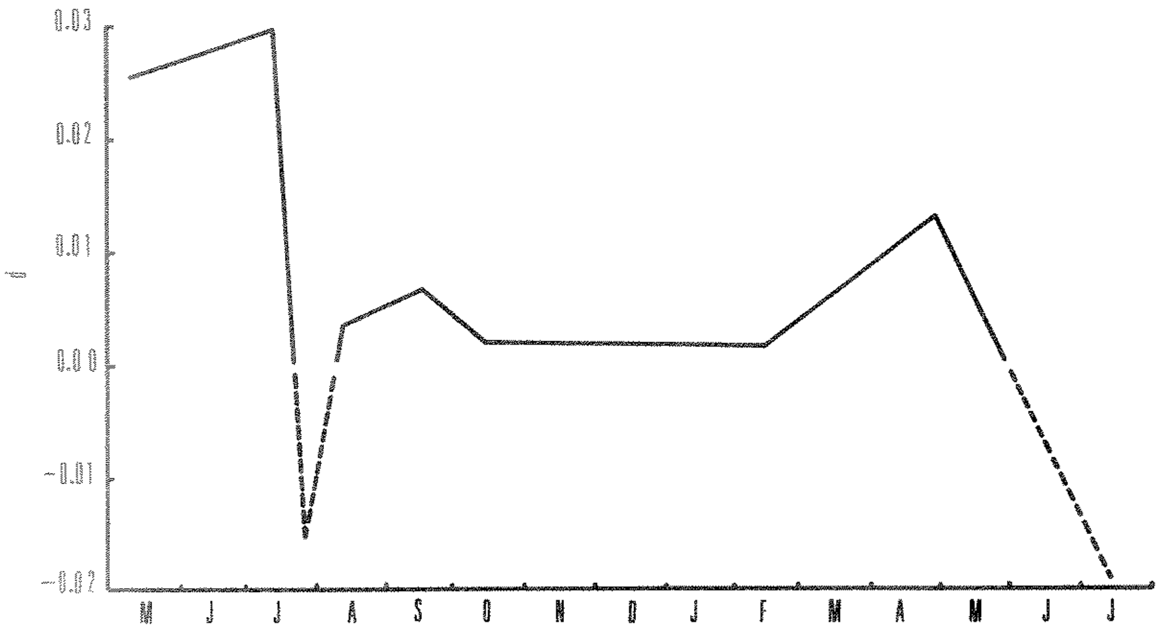


Figure 15. Mortality rate coefficient for a population of Pisidium compressum, May, 1964, through July, 1965.

value of d was obtained. This is obviously impossible, and probably results from sampling error. Mortality was generally highest during the spring high water periods (approximately May 1 to July 1), with an average mortality rate coefficient of 0.0212. Average values of d were 0.0061 for summer and 0.0016 for winter. An estimate of d was also obtained by following a cohort of Pisidium through the summer of 1964, assuming an average growth rate coefficient of 0.0188. This yielded a value of d = 0.0074.

Growth rate coefficients (g) were determined from field data, and from data obtained by rearing individuals in plastic screen cages anchored in the stream. During winter months reproduction and mortality were low, and growth calculated from total population data yielded an average of g = 0.0027 (Fig. 16). An attempt was made to follow growth by size-

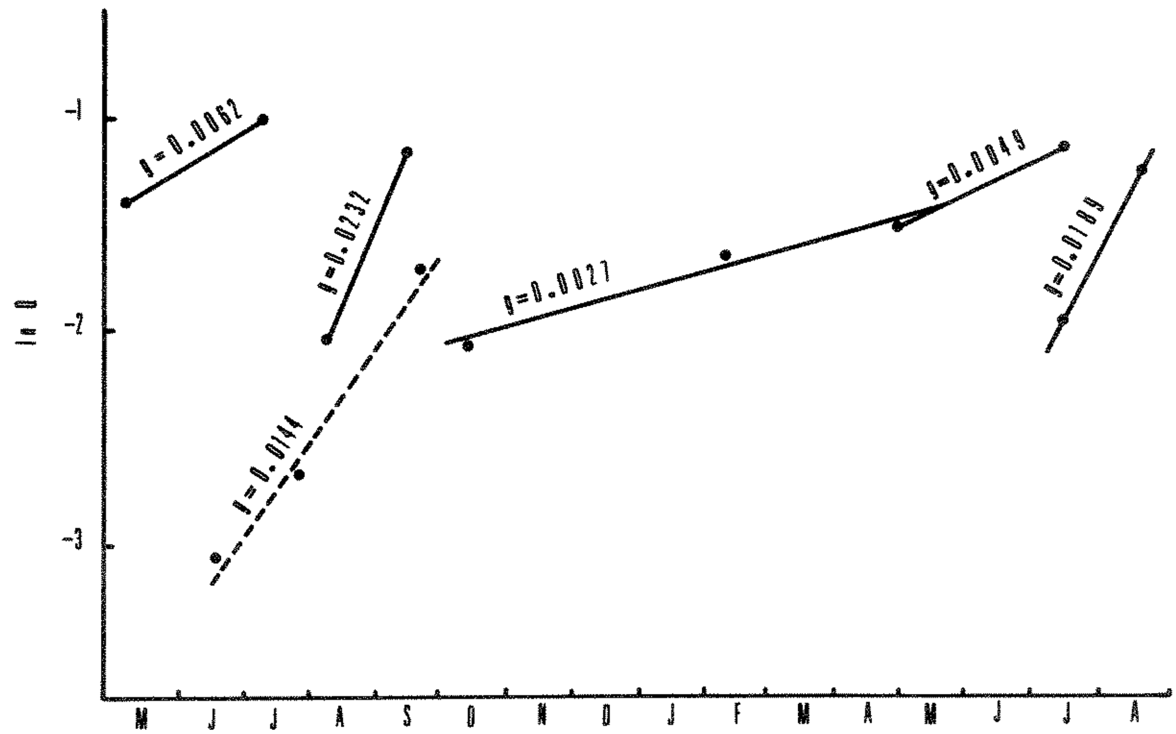


Figure 16. Growth curves for Pisidium compressum, May, 1964, through April, 1965. Captive population - broken line; natural population - solid line.

frequency analyses during spring and summer of both 1964 and 1965. Spring values were g = 0.0062 in 1964 and g = 0.0049 in 1965. Summer values were g = 0.0232 in 1964, and g = 0.0189 in 1965. Data for captive individuals yielded a value of $g = 0.0144$. The average of these summer values was 0.0188.

A growth-survivorship curve (Fig. 17) was constructed from data on a

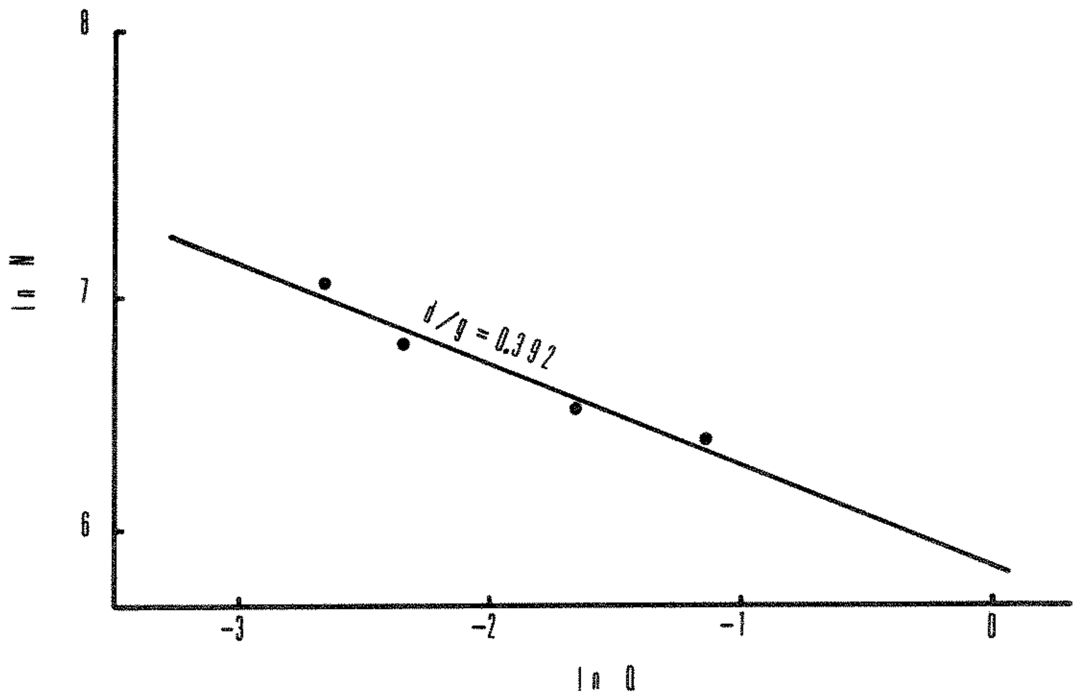


Figure 17. Growth-mortality curve for a population of Pisidium compressum.

cohort of animals followed through the summer of 1964 by size-frequency analyses. This curve, which represented an estimated initial population ($N_o$) of 1320, was fitted to equation 13, giving a value of $d/g = 0.392$. The curve was integrated planimetrically to yield a net production of 416.39 mg ($P_c$), or 0.3154 mg per individual born into the population ($P_i$).

Using this value, and an estimated value of $B' = 9569/m^2$, total net production was calculated at 3018.06 $mg/m^2$ by equation 16. Using a value of $d/g = 0.593$, obtained from winter field data, and estimated values of $N_o = 9569$ and $Q_o = 0.038$ mg, equation 14 yielded a calculated net production of 2611.27 $mg/m^2$. These calculations do not take into account the high mortality which occurs in spring, and so may overestimate the actual net production.

## DISCUSSION

Statistical evaluation of natural populations is more difficult than for laboratory populations, and is consequently subject to greater error. Nevertheless, as pointed out by Wright (1965), measurement of the dynamics of natural populations is necessary for an understanding of productivity relationships in aquatic ecosystems. Population statistics based on relatively simple exponential functions are less precise than those based on more complex models, but are generally adequate for description of the processes studied (Cole, 1954). Hall (1964) has suggested that simple exponential models may be useful in testing the effects of particular environmental variables, although they are of little value in forecasting population changes.

Allen (1951) pointed out that estimation of production by determining the area under a growth-survivorship curve is a more accurate method than using the product of mean population biomass and the number of population "turn-overs". He indicated that the latter method, which has been used by Juday (1940), Lindeman (1941), Wright (1965), and others, yields an underestimate of actual production. The model growth-survivorship curve, proposed by Neess and Dugdale (1959) has the advantages of allowing direct calculation of production from population statistics, and permitting the estimation, by interpolation or extrapolation, of points on the curve for which data are unavailable. In addition, this model is based upon simple exponential growth and mortality functions, and may be used with data commonly collected in studies of populations. On the other hand, the model is essentially empirical and may or may not be applicable to a particular population. It requires that the ratio d/g remain constant, which will be true only if mortality and growth rate respond to environmental variations in the same way.

In the present study, data fitted to the model population curve showed good fit for all species. Goodness of fit was tested by a chi-square test, using (n - 3) degrees of freedom for n observations. Probabilities that the data fit the model were as follows: *Physa*, $P > 0.990$; *Gyraulus*, $P > 0.900$; *Valvata*, $P > 0.975$; *Pisidium*, $P > 0.950$. Production calculated by equation 14 was compared with that calculated by planimetering the area under the growth-survivorship curves, which is not dependent upon the fit of the model. Total annual net production for all species was 7.575 $g/m^2$ by equation 14, within ten percent of the value of 8.354 $g/m^2$ calculated by planimetry. This was less than the difference expected from sampling error. There was a tendency for data on adult populations to depart from the model in spring and early summer, when increased mortality due to high water conditions and proportionately large numbers of senescent individuals in the population was not accompanied by increased growth. There was also a tendency for a departure from the model when populations were largely made up of very young individuals, but data were not adequate to show this clearly. It is possible that growth rates, especially in young animals, increased more sharply with temperature than did mortality rates. It appears that the Neess - Dugdale model is adequate, within the limits of sampling error, for calculating net production of the species included in this study. However, estimates of reproduction obtained by extrapolation ($N_o$ on the growth-mortality curve) differed significantly from those obtained by calculation of B' by equation 9.

Mortality rates showed a general correlation with temperature (Fig. 18) but were affected by other factors, especially high water and aging within the populations. The principal temperature-correlated cause of mortality was probably predation. Remains of snails and fingernail clams were found in fish stomachs, although no detailed stomach analyses were made. The mollusks may also have fallen prey to waterfowl and such invertebrates as leeches. There was no indication that other temperature-correlated causes of mortality, such as disease or parasitism, were important. Very high mortality of adult Gyraulus and Valvata was observed in spring and early summer. This appeared to result from a combination of high water and physiological aging. Many adults of these species apparently died shortly after reproducing. Mortality of Physa was much higher in the spring of 1964 than in 1965. Immigration of adults into the study area in spring and early summer of 1965 may have reduced the observed mortality of Physa. Mortality of Pisidium also increased during high water periods, but high summer mortality of adults was less obvious. Mortality

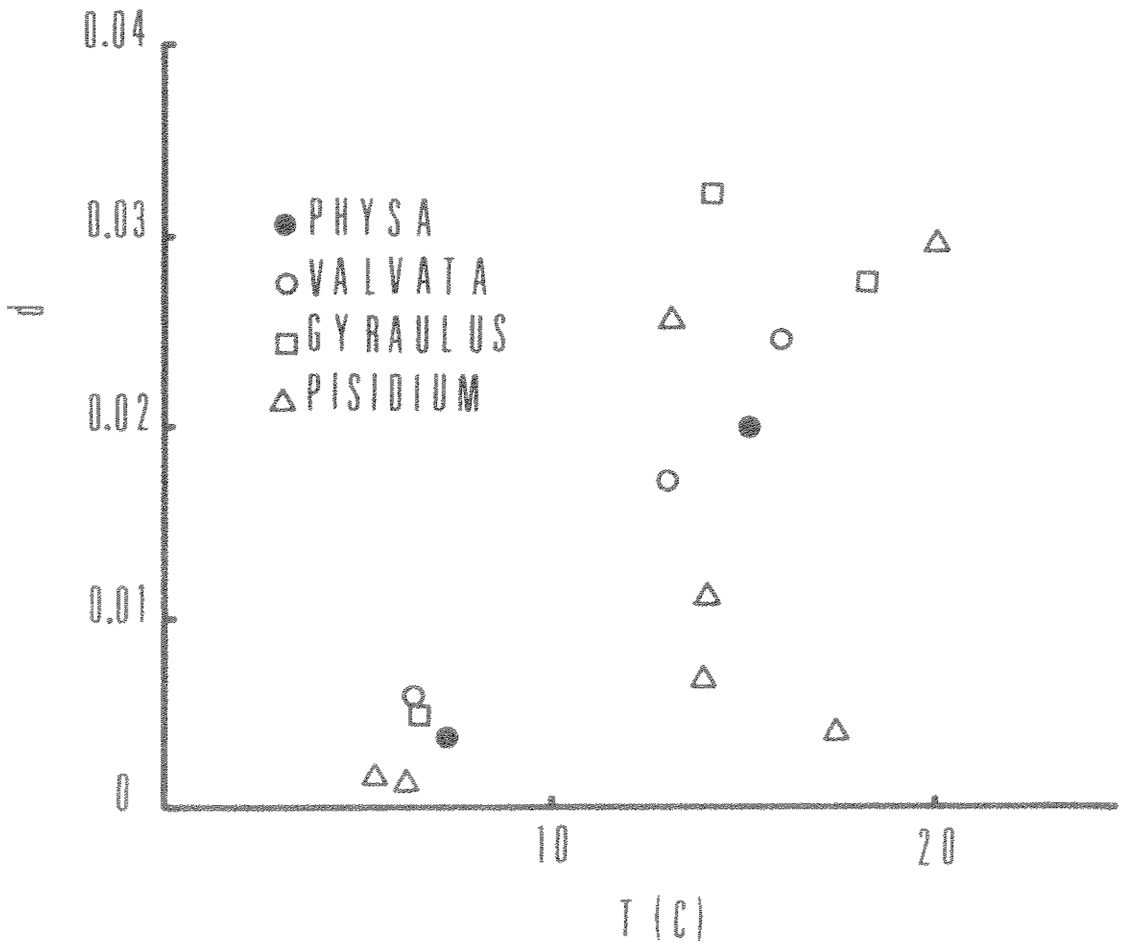


Figure 18. Average mortality rate coefficients (d) versus temperature for four species of mollusks.

rates of Physa, Valvata, and Pisidium showed a positive correlation with population number during the two high water periods (Fig. 19), and mortality caused by high water appears to be at least partly density-dependent for these species. Data were not adequate to show this correlation for Gyraulus. Heaton (1966) found large numbers of Gyraulus deflectus, Physa gyrina, and Pisidium casertanum in spring and early summer drift samples

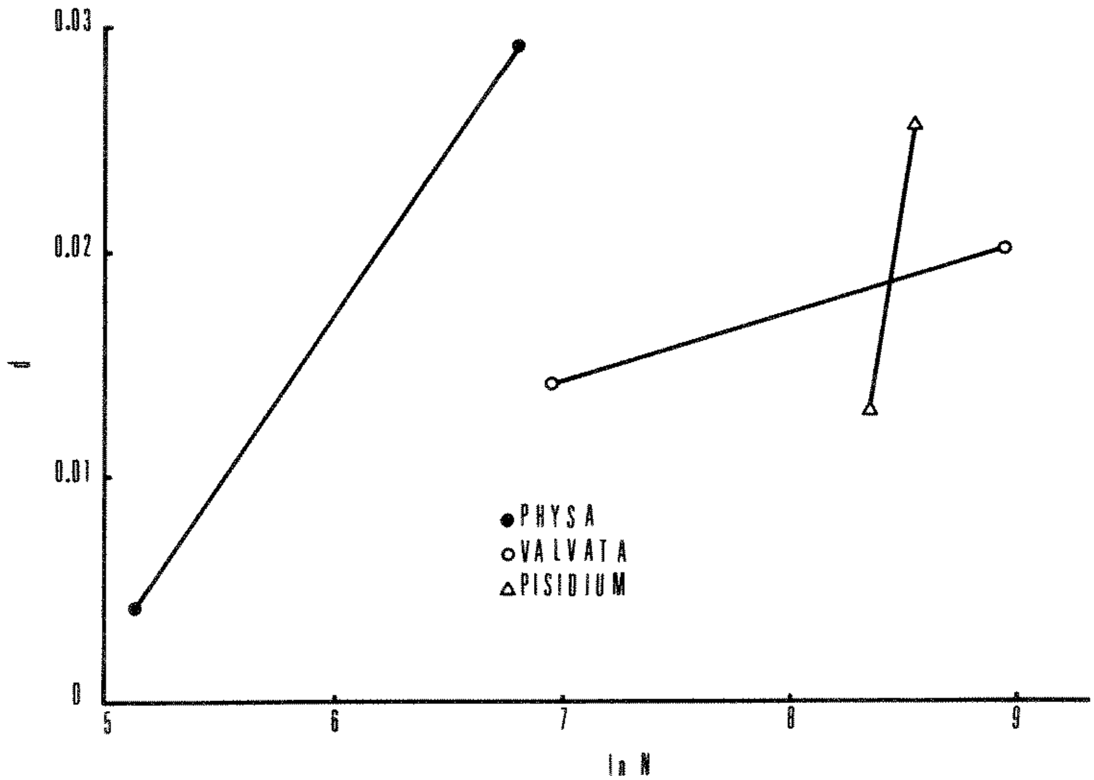


Figure 19. Mortality rate coefficients (d) versus population number (N) during high water periods for populations of Physa gyrina, Valvata humeralis, and Pisidium compressum.

taken at a station eleven kilometers downstream from my study area. The latter two species were also found throughout the year in benthos samples taken at the drift station.

Valvata had the highest growth rate observed during the study (g = 0.0333) and Gyraulus the highest growth rate in winter (g = 0.0064). Temperature and the age of individuals appeared to be the major factors influencing growth rates within species. All species showed great variations of growth rate with temperature (Fig. 20). Growth of mature animals

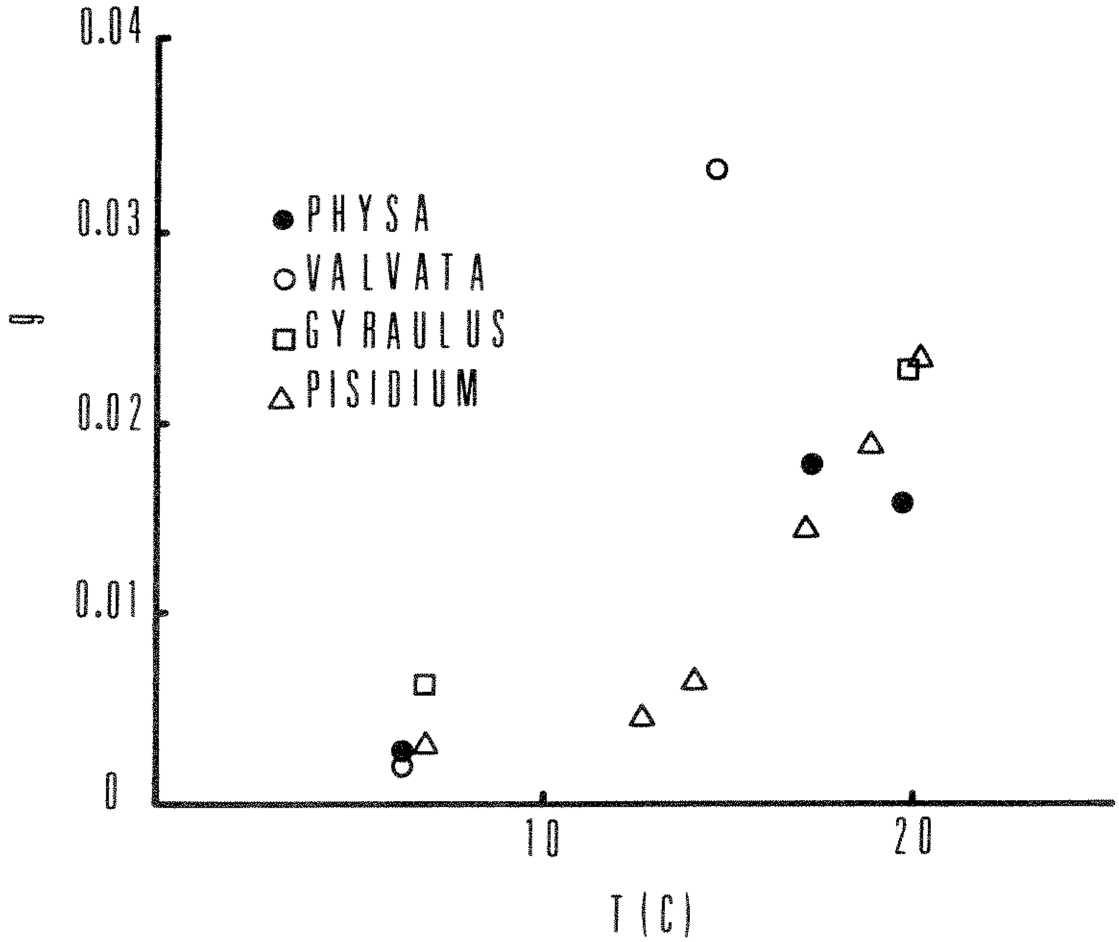


Figure 20. Average growth rate coefficients (g) versus temperature for four species of mollusks.

was much slower than that of young animals even at summer temperatures. DeWitt (1954a), Tsikhon - Lukanina (1963), and others have reported sigmoid growth curves for mollusks, with growth slowing as the animals neared maturity. There was no evidence that food supply limited growth of any species. All species of gastropods apparently reached maturity in one year, although some Physa probably survived the second winter. Pisidium appeared to be at least partly biennial. Individuals born in late summer and fall did not reach maturity until after their second winter, while those born in spring probably matured in summer of the following year. There was no evidence of separate annual and biennial populations. Individual differences seemed to depend entirely on date of birth.

Reproduction extended over several months for all species except Valvata, which reproduced during approximately one month. Reproduction of Gyraulus appeared to be concentrated into a shorter period in 1965 than in 1964. The greatest reproductive rate, which was correlated with shortest reproductive period, occurred in Valvata ($b = 0.1194$). Maximum reproductive rates were reached in July for all species except Valvata.

Maximum and minimum populations of Physa and Pisidium were approximately the same for the two summers, but Gyraulus appeared to increase and Valvata to decrease over this period (Fig. 21). These two latter species may be competitive, since Valvata decreased in numbers as Gyraulus increased. Such apparent trends may be misleading, considering that the study period covered less than two full cycles of the populations.

The total annual net production of gastropods was calculated to be 5.336 g/$m^2$ by planimetry and 4.964 g/$m^2$ by equation 14, with an average value of 5.150 g/$m^2$. This is equivalent to 21,949 g cal/$m^2$, assuming a value of 4262 g cal/g dry weight of mollusk tissue, obtained by averaging several values reported in the literature (Golley, 1961; Paine, 1965). The average net production of Pisidium was 2.815 g/$m^2$, or 11,998 g cal/$m^2$.

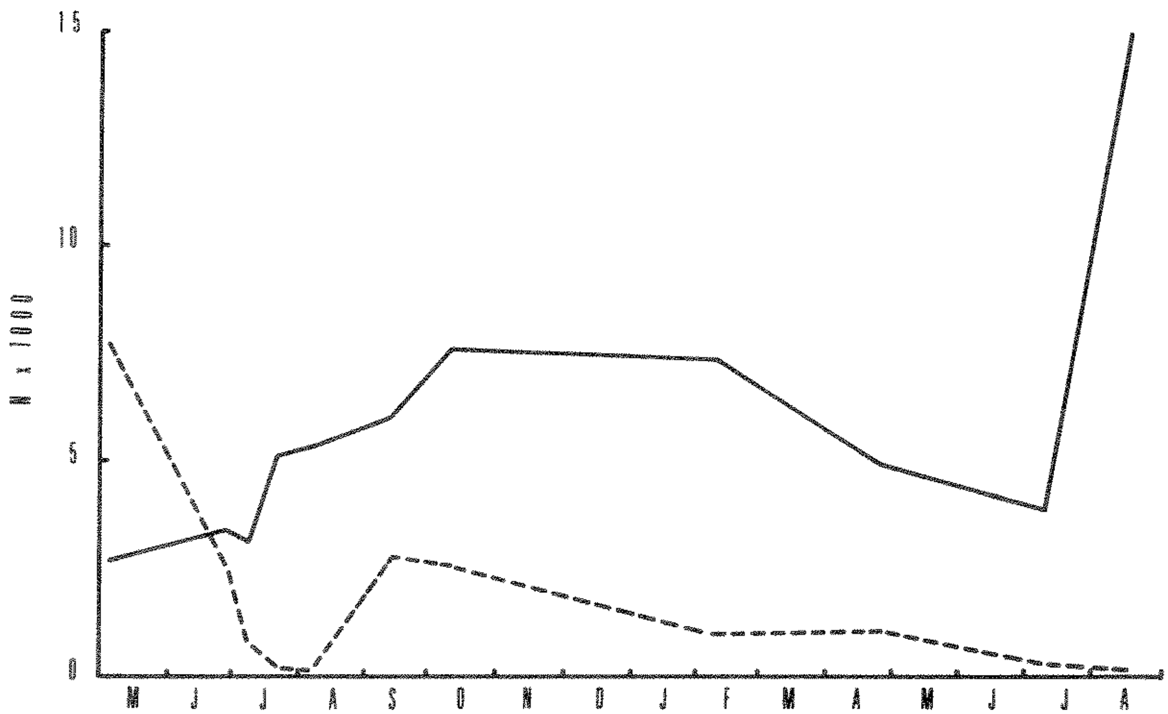


Figure 21. Populations of Gyraulus deflectus (solid line) and Valvata humeralis (broken line) May, 1964, through August, 1965.

Teal's (1957) efficiency value of 0.25 for all herbivores is assumed to apply to the gastropods, and his value of 0.47 for Pisidium virginicum is assumed to apply to Pisidium compressum, total annual assimilation of the gastropod populations was 87,796 g cal/m$^2$, and that of the Pisidium population was 25,527 g cal/m$^2$ (Total: 113,323 g cal/m$^2$). The above value for total gastropod assimilation is equivalent to 21.41 g/m$^2$ of plant material, assuming a calorie content of 4100 g cal/g dry weight of plants. Plants were collected along with mollusks in the same samples and dry weights were estimated, exclusive of roots. The standing crop of

Potamogeton spp. increased from 86.6 g/m$^2$ in April, 1965, to 276.0 g/m$^2$ in August, 1965, so that the minimum net production of plant material was 183.4 g/m$^2$. The actual growth probably exceeded 200 g/m$^2$. Thus the gastropods, if they fed exclusively on Potamogeton, assimilated approximately ten percent of the available net primary production. All other invertebrate herbivores combined probably consumed no more than the gastropods, while such vertebrates as muskrats and waterfowl consumed an undetermined amount. It appeared that at least fifty percent of the net production of the Potamogeton beds was converted into muck by bacterial action.

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