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

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POPULATION STUDIES OF FOUR SPECIES OF MOLLUSCS IN THE MADISON RIVER, YELLOWSTONE NATIONAL PARK[1]

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ABSTRACT

Population statistics were calculated for natural populations of *Physa gyrina*, *Gyraulus deflectus*, *Valvata humeralis*, and *Pisidium compressum*.

Total net production calculated for model populations was within 10% of the value calculated graphically. Data showed a generally good fit to the model curve. The average of the two methods of determining total annual net production of the gastropods was 5.150 g/m^2. Assuming an efficiency of 0.25, total gastropod assimilation was approximately 10% of the annual net primary production. Growth rates apparently were not limited by food supply. Mortality rates were highest in spring and summer and lowest in winter with the principal causes predation and loss during high water. Reproductive periods of *Physa*, *Gyraulus*, and *Pisidium* extended from spring to fall; *Valvata* reproduction was largely limited to August.

INTRODUCTION

Populations of four species of molluscs in a bed of aquatic macrophytes were analyzed on the basis of samples taken over a 17-month period (April 1964 to August 1965): three gastropods—*Gyraulus deflectus* (Say), *Physa gyrina* Say, and *Valvata humeralis* Say; and one pelecypod —*Pisidium compressum* Prime. From these samples and from laboratory experiments, growth rate, birth rate, death rate, rate of population change, and production were estimated.

DeWitt (1954*a*,*b*, 1955) has studied the ecology of *Physa gyrina*, and Clampitt (1963), Heard (1963), and Thomas (1959, 1963) investigated population dynamics of species closely related to those I have considered.

This investigation was confined to a section of the Madison River 15.1 km upriver from the west boundary of Yellowstone National Park. The Madison River is formed by the confluence of the Firehole and Gibbon rivers, both of which receive thermal water from geysers and hot springs. As a result, its temperature (Fig. 1) is higher than that of most Northern Rocky Mountain streams at a similar altitude (2,046 m). No ice was observed at the study area. The water is high in dissolved solids and alkalinity, but low in divalent cations (Table 1). Silicate is high, but it appears to be largely in undissociated form.

The study area was 150 m long; a channel about 15 m wide and 2 m deep was flanked on each side by shallows with a maximum depth of 1 m, covered by a heavy growth of aquatic plants (Fig. 2). Surface current in late summer varied from about 1 m/sec in midchannel to less than 1 cm/sec in the beds of vegetation. In late winter, when the plants had died down, surface current over the shallows increased to 15–20 cm/sec and went up to

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

	Range	Mean
Conductivity ($K_{25} \times 10^6$)	274–488	424
Alkalinity (meq/liter)	1.25–2.50	2.13
Calcium (meq/liter)	0.09–0.21	0.14
Magnesium (meq/liter)	0.00–0.10	0.04
Potassium (meq/liter)	0.12–0.28	0.28
Sodium (meq/liter)	2.10–4.80	3.82
Chloride (meq/liter)	0.89–1.83	1.58
Sulfate (meq/liter)	0.41–0.46	0.44
Phosphate (meq/liter)	0.006–0.017	0.013
Silicate (meq/liter)	2.02–2.65	2.42
pH	7.30–7.89	7.60

50 cm/sec during the high water stage (about 1 May to 1 July in 1964 and about 1 May to 20 July in 1965). The study area is separated from similar habitats above and below by broad shallow riffles. Qualitative samples were taken from the entire area; quantitative samples were taken only from the shallows northwest of the channel. The bottom in the shallows was silt and muck; the bottom of the channel was bedrock covered with a thin layer of sand and gravel.

Potamogeton natans L. was the most abundant plant. It occurred in nearly pure stands, as did *P. foliosus* Raf. which covered less of the area (Fig. 2). Other macrophytes were *Ranunculus aquatilus* L., *Hippurus vulgaris* L., *Eleocharis* sp., *Sparganium* sp., *Myriophyllum exalbescens* Fern., *Utricularia* sp., *Potamogeton filiformis* Pers., *Zannichellia palustris* L., and *Chara* sp.

METHODS

Organisms were collected with a mechanical sampler (Gillespie and Brown 1966), consisting of a 0.1-m² frame with an attached net and a gear-driven closing mechanism. Mesh size averaged 0.8 × 0.7 mm, permitting significant losses of newly hatched individuals of some species. Correction factors were applied when necessary; these were determined by placing known numbers of small size molluscs (class I *see below*) in the sampler net with silt and vegetation, washing as in the field collections, and counting to find the proportion lost. Collections for each date were taken along transects, with each transect located upstream from the previous ones 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 *P. natans* or *P. foliosus* were used. This resulted in stratification of sampling for both plant type and depth (0.5–1.0 m).

Each sample was removed from the sampler, placed in a plastic bag and preserved in 5% formalin. In the laboratory, samples were rinsed free of formalin, and the macroinvertebrates were separated from plant material and detritus, sorted by species, and preserved in 70% ethanol. The selected species were then sorted into size classes I, II, III, and IV (from smallest to largest) and counted. Fingernail clams (*Pisidium*) were sized by sorting on a grid under a microscope, and snails were washed through a series of graded screens. Adult fingernail clams were dissected and embryos counted. All molluscs were decalcified with 0.5 N HCl, dried to constant weight at 65C, and weighed to the nearest 0.1 mg. The small error introduced by this procedure was ignored (Richards and Richards 1965).

Population number per square meter (N), population biomass (W in mg/m²) and mean individual biomass (Q in mg) were estimated from collection data. Drift into and out of the study area was found to be negligible in limited sampling, and immigration and emigration were assumed to be balanced. Population statistics for rate of population change, birth rate, and mortality rate were calculated from the equation:

$$r = b - d = \mathrm{d}N/N\,\mathrm{d}t, \qquad (1)$$

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

$$N_t = N_0 e^{(b-d)t}, \qquad (2)$$

where e is the base of natural logarithms, N_t is the population at the time of collection, and N_0 is the population at the previous collection. Taking the natural logarithms of both sides and rearranging:

$$b - d = (\ln N_t - \ln N_0)/t. \qquad (3)$$

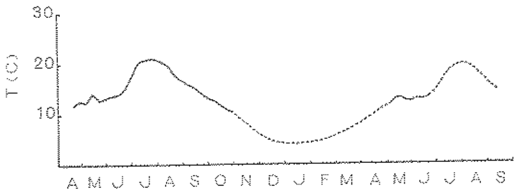

FIG. 1. Average temperatures in Madison River April 1964 to September 1965. Solid line from thermograph data furnished by J. C. Wright. Dotted line estimated from maximum-minimum and pocket thermometer data.

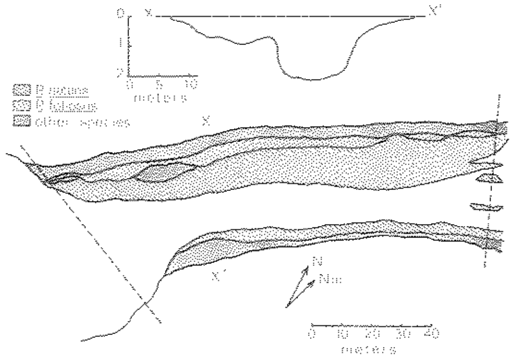

FIG. 2. Madison River study area, showing cross section through X–X' and distribution of plants.

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 subject to the judgment of the investigator—especially with regard to selection of size classes. Nevertheless, it probably gives 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 hatching rate was calculated from:

$$b = r + d. \qquad (4)$$

No data on egg production or mortality were collected.

The population of *P. 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:

$$B = E/t', \qquad (5)$$

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; 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:

$$b = \ln (B + 1); \qquad (6)$$

r was determined from population data, and d was calculated using equation (4). Total reproduction (B') over a period of time was calculated by:

$$B' = \sum_{x=1}^{y} \bar{N}_x B_x t_x, \qquad (7)$$

where $\bar{N}_x$ 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:

$$\mathrm{d}Q/\mathrm{d}t = gQ, \qquad (8)$$

TABLE 2. *Population data for* Physa gyrina, *showing No./m² (N), standard error (SE), population biomass in mg/m² (W), per cent of population in size classes I (smallest) through IV (largest), and coefficients of rates of population change (r), reproduction (b), and mortality (d)*

Date	$N \pm$ SE	W	Per cent I	II	III	IV	r	b	d
1964									
5 May	894 ± 100.5	791.0	1.6	38.3	47.6	12.5	–0.0292	0.0000	0.0292
28 Jun	185 ± 69.9	213.5	0.0	18.9	64.9	16.2	0.0548	0.0745	0.0197
7 Jul	303 ± 74.4	593.6	1.3	16.2	28.4	54.1	0.0394	0.0591	0.0197
21 Jul	526 ± 77.3	496.3	47.5	19.8	6.5	26.2	0.0812	0.1009	0.0197
6 Aug	1,928 ± 833.7	654.0	40.0	45.6	10.9	3.5	–0.0107	0.0090	0.0197
12 Sep	1,296 ± 377.4	724.3	14.5	47.1	28.1	10.3	–0.0197	0.0000	0.0197
9 Oct	762 ± 307.9	473.3	24.7	35.8	23.4	16.1	–0.0041	0.0001	0.0042
1965									
7 Feb	466 ± 238.1	213.7	41.3	39.8	11.4	7.5	–0.0132	–0.0090	0.0042
25 Apr	168 ± 64.0	205.4	1.2	16.7	46.4	35.7	0.0056	0.0098	0.0042
9 Jul	255 ± 34.6	157.6	20.8	47.0	17.3	14.9	0.0613	0.0810	0.0197
16 Aug	2,460 ± 309.1	1,372.8	32.6	42.9	15.6	8.9			

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:

$$g = (\ln Q_t - \ln Q_0)/t, \tag{9}$$

where Q_t is mean individual weight at time of an observation, and Q_0 is mean individual weight at the time of an observation t days earlier. 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 of Allen (1951) and 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:

$$P_n = \int_{Q_0}^{Q_t} N \, dQ. \tag{10}$$

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:

$$\ln N_t = \ln N_0 + d/g\,(\ln Q_0 - \ln Q_t). \tag{11}$$

Since N is given as a function of Q, production is obtained by integrating equation (10):

$$P_n = N_0 Q_0^{k}(1-k)^{-1}(Q_t^{1-k} - Q_0^{1-k}), \tag{12}$$

where k is the constant d/g, and Q_t is the mean individual weight of adult animals. This model implies that mortality and growth vary seasonally in the same manner, so that d/g is constant, while the graphic method yields a value of P_n independent of the relationship of d and g. The estimated values of N_0 differed somewhat for the two methods, since N_0 for the graphic method was calculated as reproduction over a period of time (B'), and N_0 for equation (12) was obtained by extrapolating the fitted curve.

This method of obtaining P_n was applied directly to the populations of gastropods, which were treated as cohorts. For the fingernail clams, the method was modified. Estimates of the growth-survivorship curve were obtained by following a size class of individuals through their life cycle 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_0, the estimated number at birth (obtained by extrapolation) in the growth-survivorship curve. The production per individual born into the population was computed as:

$$P_i = P_c/N_0 = 1/N_0 \int_{Q_0}^{Q_t} N \, dQ. \tag{13}$$

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

$$P_n = B' P_i, \tag{14}$$

where B' is calculated from equation (7).

RESULTS

Physa gyrina

Examination of population data (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 from June to August in 1964 was accompanied by a shift in population structure from 81.1% adults (classes III and IV) to 85.6% juveniles (classes I and II). Reproduction occurred from July through October with a peak in July. Those individuals hatched after 7 July and before 6 August made up an estimated 78% of the 1964 generation; an attempt was made to follow the life history of this cohort by size-frequency analyses. Population and weight estimates were used to calculate mortality and growth rates (Table 3).

The survivorship curve obtained was fitted to equation (3), with b considered equal to zero and average value of d determined from the slope. The best fit was obtained by dividing the curve into two parts with a d coefficient 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 it 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 habitats. The high apparent mortality in fall may have resulted from dispersal out of the study area. The coefficient b was determined for intervals between samples (equation 4), using the average values of d for each time of year (Table 2). The maximum observed value of b was 0.1009 (21 Jul–6 Aug 1964), corresponding to a finite hatching rate of 0.1062 individuals per individual per day (equation 6). The total number of individuals introduced into the population (B') during 1964 was 3,133.

TABLE 3. *Population data for a cohort of* Physa gyrina, *showing No./m² (N), mortality rate coefficient (d), mean individual biomass (Q), and growth rate coefficient (g)*

Date	N	d	Q	g
1964				
21 Jul	250	—	0.094	0.0453
6 Aug	1,650	0.0269	0.194	0.0128
12 Sep	610	0.0112	0.312	0.0132
9 Oct	451	0.0135	0.446	0.0140
1965				
7 Feb	88	0.0050	1.575	0.0043
25 Apr	60	0.0061	2.196	0.0002
9 Jul	38	–0.0462	2.220	0.0067
16 Aug	220		2.860	

A growth curve was constructed from the mean weight data, fitted to equation (8), and the coefficient g was determined from the slope. Growth rate is expected to vary, but a reasonably good fit was obtained by breaking the data into two sections corresponding to the two parts of the survivorship curve. This gave values for g of 0.0179 in summer and fall and of 0.0027 in winter and spring. The g coefficient of individuals raised in aquaria at a mean temperature of 19.5C averaged 0.0159. DeWitt's (1954*a*) data yield a much higher value ($g = 0.136$) than any of the above, but this is only an approximation, since his growth data were converted from shell length to shell-free dry weight for comparison with my results.

Survivorship and growth data were combined (Fig. 3) and fitted to Neess and Dugdale's (1959) model (equation 11). The average value of d/g obtained by the method of least squares was 1.097, with

TABLE 4. *Population data for* Gyraulus deflectus. *Symbols as in Table 2*

Date	$N \pm$ SE	W	Per cent I	II	III	IV	r	b	d
1964 5 May	2,686 ± 250.9	802.0	6.5	47.3	40.1	6.1			
							0.0046	0.0283	0.0237
28 Jun	3,436 ± 1,082.0	1,021.7	2.5	50.3	43.3	3.9			
							–0.0089	0.0234	0.0323
7 Jul	3,173 ± 471.6	856.4	15.6	42.8	39.1	2.5			
							0.0342	0.0665	0.0323
21 Jul	5,122 ± 1,803.8	850.7	47.8	38.7	13.1	0.4			
							0.0028	0.0351	0.0323
6 Aug	5,357 ± 1,115.6	492.2	67.0	30.9	1.8	0.3			
							0.0054	0.0377	0.0323
12 Sep	6,010 ± 1,531.6	396.2	66.8	32.5	0.7	0.0			
							0.0084	0.0407	0.0323
9 Oct	7,548 ± 515.8	570.2	69.2	29.5	1.2	0.1			
							–0.0002	0.0000	0.0002
1965 7 Feb	7,381 ± 738.4	1,299.7	36.3	52.0	11.2	0.5			
							–0.0053	0.0000	0.0053
25 Apr	4,926 ± 870.4	1,342.3	8.6	51.0	32.8	2.6			
							–0.0031	0.0206	0.0237
9 Jul	3,902 ± 599.8	689.7	43.9	37.2	17.6	1.3			
							0.0361	0.0684	0.0323
16 Aug	15,378 ± 3,663.0	1,329.1	65.0	34.4	0.6	0.0			

N_0 estimated at 2,754. 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 (avg 1.405).

Estimated values of $Q_0 = 0.09$ mg and $N_0 = 2{,}430$ were used to calculate net production from field data by planimetry; the value obtained was 854.50 mg/m^2. The value obtained using equation (12) was 730.07 mg/m^2 ($N_0 = 2{,}754$; $Q_0 = 0.09$; $d/g = 1.097$). Since these values were for an estimated 78% 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 thus calculated to be 1,095.51 mg/m^2 from field data, and 935.99 mg/m^2 from a model population fitted to the data.

Gyraulus deflectus

The field data (Table 4) show a low population in early summer of 1964, followed by a rather slow increase to a peak in October. Population peaks are accompanied by a changing population structure as with *Physa*. An attempt was made to follow a generation through a life cycle by size-frequency analysis, 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 population peak. In addition, newly hatched animals were able to pass through the net, so that during periods of peak reproduction, 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% of class I individuals during reproductive periods. Calculations included an estimated 81% of the 1964–1965 generation.

The survivorship curve was fitted to equation (3); b was considered equal to zero, yielding average d coefficients 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 (6 Aug–12 Sep 1964) during 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 accounted for completely. The coefficient b was calculated (equation 4), assuming that d was equal to 0.0323 during the reproductive season (Table 4). Reproduction was assumed to be zero during winter. B' was calculated to be 28,315 (equation 7).

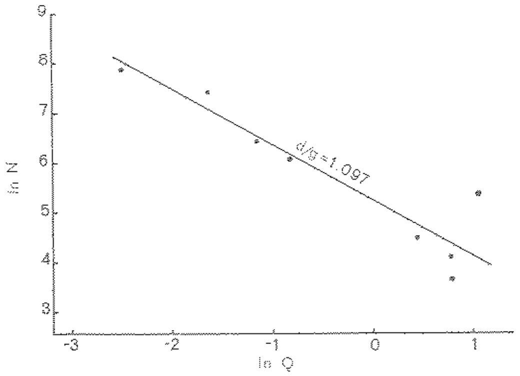

FIG. 3. Growth-mortality curve for *Physa gyrina*. Natural logarithm of No./m^2 (N) vs. natural logarithm of mean individual biomass (Q), with line of best fit (equation 12).

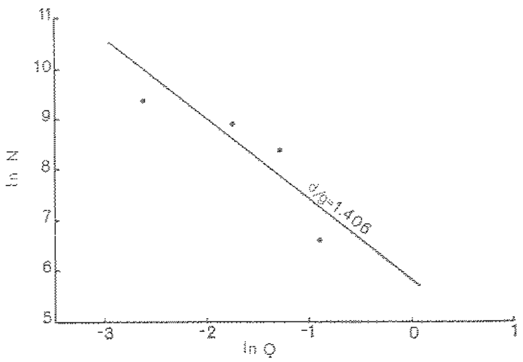

FIG. 4. Growth-mortality curve for *Gyraulus deflectus*. (*See* Fig. 4 and text for explanation.)

The growth curve yielded an average g coefficient of 0.0064 when fitted to equation (8), with no increase in spring. Data for the total population yielded almost identical growth rates ($g = 0.0065$) for the winter months (9 Oct 1964–25 Apr 1965). An approximate g coefficient for summer of 0.0230 was determined from a group of animals raised in aquaria at a mean temperature of 19.5C.

Data for growth and survivorship were combined (Fig. 4) and fitted to equation (11), 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 g coefficient for summer of 0.0230, an average summer value for d of 0.0323 was obtained—identical to the spring and early summer value.

Net production, which was calculated from field data by planimetry using estimated values of $Q_0 = 0.037$ mg and $N_0 = 22{,}935$, was 2,708.25 mg/m^2. The value of P_n calculated by equation (12), with $Q_0 = 0.037$ mg, $N_0 = 40{,}120$, and $d/g = 1.406$, was 2,453.06 mg/m^2. Since these values were for an estimated 81% of the 1964–1965 generation, total net production calculated from field data was 3,343.52 mg/m^2, and the value calculated for a model population fitted to the data was 3,028.47 mg/m^2.

Valvata humeralis

The data (Table 6) show a population 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. Calculation of population statistics were 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.

TABLE 5. *Population data for a cohort of* Gyraulus deflectus. *Symbols as in Table 3*

Date	N	d	Q	g
1964 9 Oct	11,500*		0.073	
		0.0037		0.0072
1965 7 Feb	7,343		0.174	
		0.0068		0.0061
25 Apr	4,374		0.278	
		0.0237		0.0051
9 Jul	736		0.408	
		0.0533		0.0079
16 Aug	97		0.551	

* Corrected for losses through net.

Table 6. *Population data for* Valvata humeralis. *Symbols as in Table 2*

Date	$N \pm$ SE	W	Per cent I	II	III	IV	r	b	d
1964									
5 May	7,686 ± 799.4	2,670.6	4.0	84.5	11.4	0.1	–0.0202	0.0000	0.0202
28 Jun	2,583 ± 666.1	921.9	2.1	76.0	21.1	0.8	–0.1196	0.0000	0.1196
7 Jul	880 ± 204.6	328.6	0.5	65.2	33.6	0.7	–0.1022	0.0000	0.1022
21 Jul	210 ± 72.9	74.2	4.8	70.5	24.7	0.0	–0.0589	0.0000	0.0589
6 Aug	82 ± 29.0	20.0	35.4	58.5	6.1	0.0	0.0948	0.1194	0.0246
12 Sep	2,738 ± 699.0	271.2	86.5	13.1	0.3	0.1	–0.0026	0.0000	0.0026
9 Oct	2,553 ± 482.3	563.4	44.9	53.0	2.1	0.0	–0.0078	0.0000	0.0078
1965									
7 Feb	997 ± 118.7	275.0	27.1	68.9	4.0	0.0	0.0007	0.0000	–0.0007
25 Apr	1,052 ± 174.0	345.7	7.8	84.2	8.0	0.0	–0.0141	0.0000	0.0141
9 Jul	366 ± 65.7	132.3	1.6	72.7	25.7	0.0	–0.0319	0.0185	0.0504
16 Aug	109 ± 23.7	24.2	50.5	35.8	7.3	6.4			

Newly hatched individuals could pass through the net, and data used in calculations (Table 7) were corrected assuming a 40% loss of class I individuals during the reproductive period. Calculations were assumed to include the entire 1964–1965 generation.

The survivorship curve, fitted to equation (3), yielded average d coefficients 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 (12 Sep 1964–9 Jul 1965), with an average value for d of 0.0073. The coefficient b for the reproductive period, using the average d value (0.0246) for the 25 April–16 August 1965 period, was 0.1199—equivalent to a B rate of 0.132, and a B' of 6,886 individuals/m².

The growth curve showed a rapid rate ($g = 0.0333$) during autumn (Sep–Oct) and a very slow rate ($g = 0.0018$) during the rest of the year. No increase in growth rate of adults was observed in spring and summer. The growth rate coefficient was 0.0550 for individuals raised in aquaria at a mean temperature of 19.5C.

The growth-survivorship curve (Fig. 5) was fitted to equation (11), yielding a calculated average value for d/g of 1.461. The average d coefficient was calculated to be 0.0486, assuming a constant ratio d/g and an average g coefficient of 0.0333 during the reproductive period. This value for d is considerably higher than the value used above and could give a correspondingly higher birth rate for the reproductive period ($b = 0.1434$).

Net production, calculated by planimetry from field data, using estimated values of $Q_0 = 0.041$ mg and $N_0 = 6{,}886$, was 897.00 mg/m². Net production was 999.61 mg/m² for a model population fitted to the data using equation (12) with estimated values of $Q_0 = 0.041$, $N_0 = 16{,}564$, and $d/g = 1.461$.

Pisidium compressum

The population of *Pisidium* was made up almost entirely of *P. compressum* and was treated as a monospecific population. Although some *P. casertanum* were included in the population, there were too few to have any significant effect on the 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, no data were collected after August, so further increases may have occurred. Maximum biomass was reached in late April or early May, just before the high-water stage of the river, and minimum biomass occurred just after high water. The distribution of *Pisidium* was 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.

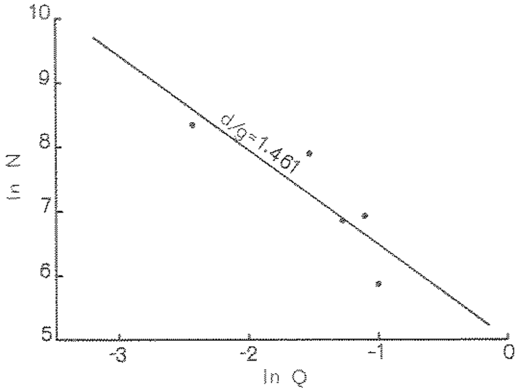

Fig. 5. Growth-mortality curve for *Valvata humeralis.* (*See* Fig. 4 and text for explanation.)

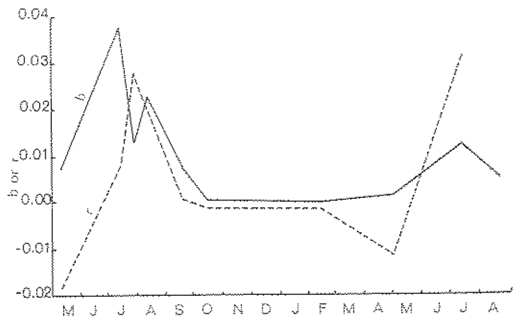

Fig. 6. Coefficients of reproduction rate (*b*, solid line) and rate of population change (*r*, broken line) for *Pisidium compressum*, May 1964 through August 1965.

Population data were used to calculate coefficients of r for each sampling period (Table 8 and Fig. 6) using equation (1). The b coefficients were calculated (equation 6) from the B values obtained with equation (5). The t' was difficult to determine accurately, since growing embryos could not be observed inside the adults. It 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 (Jul–Sep). An estimated value of $t' = 16$ days was used to calculate B for spring and fall collections. The estimated B' for 1964 was 9,569 (equation 7).

The reproductive period for this species was lengthy, extending from late April through October with maximum reproduction occurring in early July. As a result, size class I was the most numerous in all but one collection (Table 8), and only one collection (7 Feb 1965) contained no embryos.

On two collection dates (21 Jul 1964 and 9 Jul 1965), a negative value of d was obtained (Table 8 and Fig. 7). This is obviously impossible, and probably resulted from sampling error or may have been a result of immigration into the study area. Mortality was generally highest during high-water periods (approx 1 May to 1 Jul), with an average d 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 summer 1964, assuming an average g coefficient of

Table 7. *Population data for a cohort of* Valvata humeralis. *Symbols as in Table 3*

Date	N	d	Q	g
1964				
12 Sep	4,317*	0.0173	0.087	0.0333
9 Oct	2,709	0.0083	0.215	0.0021
1965				
7 Feb	997	–0.0007	0.276	0.0023
25 Apr	1,052	0.0141	0.329	0.0013
9 Jul	366	0.0504	0.362	0.0013
16 Aug	54		0.380	

* Corrected for losses through net.

TABLE 8. *Population data for* Pisidium compressum. *Symbols as in Table 2*

Date	$N \pm$ SE	W	Per cent I	II	III	IV	r	b	d
1964 5 May	5,138 ± 369.4	1,269.8	35.5	37.8	18.7	8.0	–0.0183	0.0073	0.0256
7 Jul	1,620 ± 428.9	263.8	62.5	24.5	8.9	4.1	0.0079	0.0375	0.0296
21 Jul	1,810 ± 514.4	267.6	59.6	27.3	10.7	2.4	0.0279	0.0124	–0.0155
6 Aug	2,829 ± 500.2	450.7	59.4	25.8	11.1	3.7	0.0189	0.0225	0.0036
12 Sep	5,688 ± 2,280.5	780.4	50.8	37.5	10.0	1.7	0.0006	0.0073	0.0067
9 Oct	5,781 ± 1,322.6	753.6	51.4	35.2	10.9	2.5	–0.0015	0.0003	0.0018
1965 7 Feb	4,833 ± 1,533.5	910.4	48.5	27.2	20.5	3.8	–0.0014	0.0000	0.0014
25 Apr	4,334 ± 624.3	952.4	54.0	24.6	16.2	5.2	–0.0114	0.0015	0.0129
9 Jul	1,837 ± 400.8	258.8	69.6	20.1	8.9	1.4	0.0313	0.0121	–0.0193
16 Aug	6,040 ± 1,004.4	706.2	78.7	14.8	5.5	1.0		0.0530	

0.0188. This yielded a value of $d = 0.0074$.

The g values 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 value of $g = 0.0027$. An attempt was made to follow growth by size-frequency analyses during spring and summer of both years. 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. 8) was constructed from data on a cohort of animals followed through summer 1964 by size-frequency analyses. This curve, representing an estimated initial population (N_0) of 1,320, was fitted to equation (11), 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 $B' = 9{,}569/\text{m}^2$, total net production was calculated at 3,018.06 mg/m² (equation 14). A value of $d/g = 0.593$ was obtained from winter field data, and estimated values of $N_0 = 9{,}569$ and $Q_0 = 0.038$ mg were used to calculate a net production of 2,611.27 mg/m² (equation 12). These calculations do not take into account the high mortality occurring in spring, and so they may overestimate the actual net production.

DISCUSSION

Statistical evaluation of natural populations is more difficult than for laboratory populations. Population statistics based on relatively simple exponential functions are less precise than those based on more complex models but are generally adequate for describing the processes studied (Cole 1954). Hall (1964) 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 estimating 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 (e.g., Juday 1940; Lindeman 1941; Wright 1965) 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, it is based on simple exponential growth and mortality functions and can be used with data commonly collected. On the other hand, the model is essentially empirical and requires that the ratio d/g remains constant, which will be true only if mortality and growth rate respond to environmental variations in the same way.

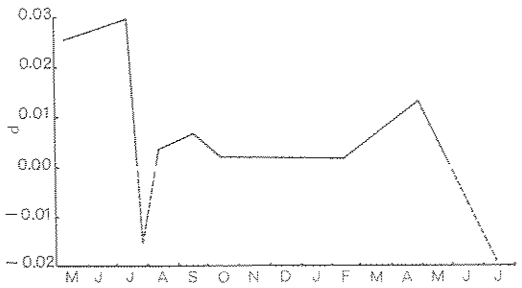

FIG. 7. Mortality rate coefficient (d) for a population of *Pisidium compressum*, May 1964 through July 1965.

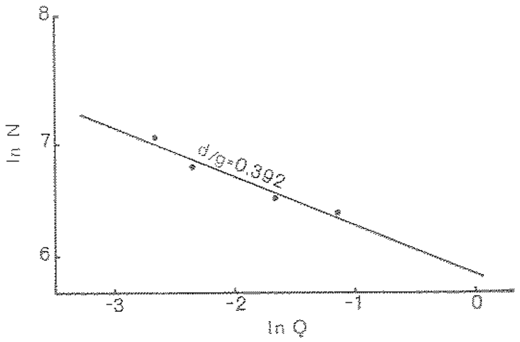

FIG. 8. Growth-mortality curve for a population of *Pisidium compressum*. (*See* Fig. 4 and text for explanation.)

In this study, data showed good fit to the model population curve for all species. Goodness of fit was tested by a chi-square test using $(n-3)$ degrees of freedom for n observations with the following results: *Physa*, $p > 0.990$; *Gyraulus*, $p > 0.900$; *Valvata*, $p > 0.975$; *Pisidium*, $p > 0.950$. As a further test, production calculated by equation (12) was compared with that calculated by planimetering the area under the growth-survivorship curves, which is not dependent on the fit of the model. Total annual net production for all species was 7.575 g/m² (equation 13)—within 10% of the value calculated by planimetry (8.354 g/m²). This was less than the difference expected from sampling error. Data on adult populations tended to depart from the model in spring and early summer when increased mortality, owing to high-water conditions and proportionately large numbers of senescent individuals in the population, was not accompanied by increased growth. There was another such tendency when populations were largely made up of very young individuals, but data were not adequate to show this clearly. Growth rates, especially in young animals, may have 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_0 on the growth-mortality curve) differed significantly from those obtained by calculation of B' (equation 7).

Mortality rates showed a general correlation with temperature (Fig. 9), but 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. High mortality of adult *Gyraulus* and *Valvata* was observed in spring and early summer, evidently the result of 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 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*

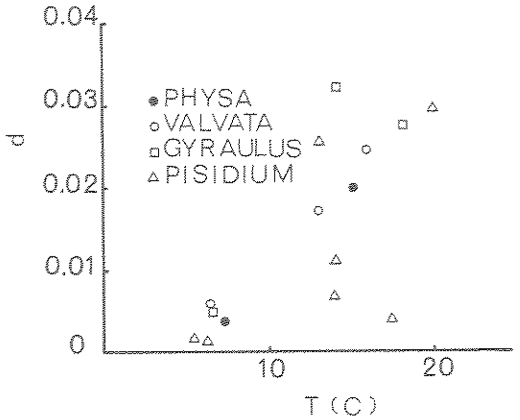

FIG. 9. Average mortality rate coefficients (d) vs. temperature for four species of molluscs.

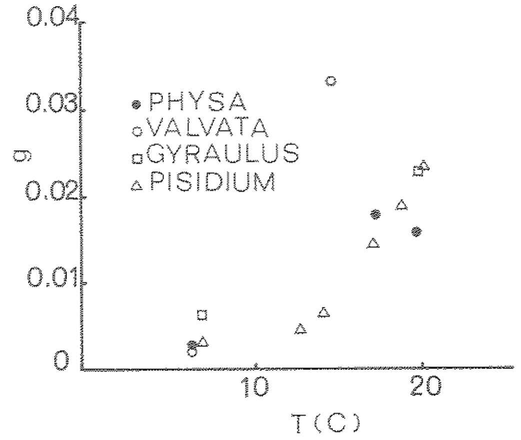

FIG. 11. Average growth rate coefficients (g) vs. temperature (T) for four species of molluscs.

also increased during high-water periods, but high mortality of adults in summer was less obvious. Mortality rates of *Physa*, *Valvata*, and *Pisidium* showed a positive correlation with population number during the two high-water periods (Fig. 10). Data were not adequate to show this correlation for *Gyraulus*. Heaton (1966) found large numbers of *Gyraulus deflectus*, *Physa gyrina*, and *Pisidium casertanum* in drift samples taken in spring and early summer at a station 11 km downstream.

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 excellent correlation of growth rate with temperature (Fig. 11). Growth of mature animals was much slower than that of young animals even at summer temperatures. DeWitt (1954*a*), Tsikhon-Lukanina (1963), and others have reported sigmoid growth curves for molluscs, 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, but 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, and individual differences seemed to depend entirely on date of birth.

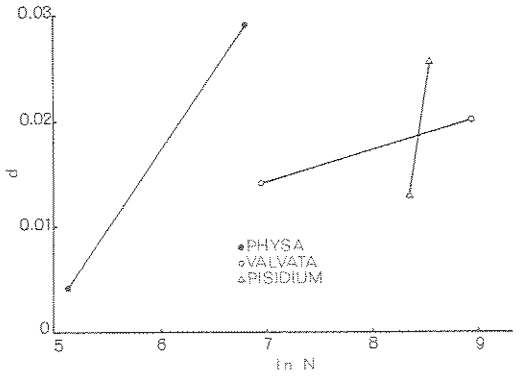

FIG. 10. Mortality rate coefficients (d) vs. natural logarithm of population number (N) during high-water periods for populations of *Physa gyrina*, *Valvata humeralis*, and *Pisidium compressum*.

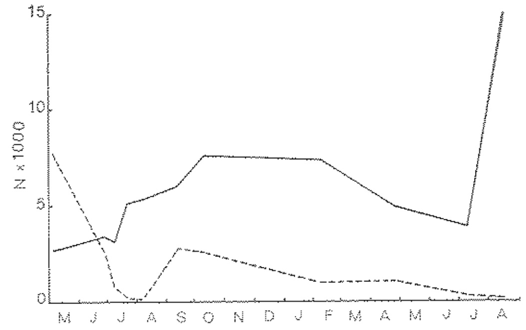

FIG. 12. Populations of *Gyraulus deflectus* (solid line) and *Valvata humeralis* (broken line), May 1964 through August 1965.

Reproduction extended over several months for all species except *Valvata*, which reproduced for 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 both summers, but *Gyraulus* appeared to increase and *Valvata* to decrease over this period (Fig. 12). Such apparent trends may be misleading, as less than two full cycles of the populations were studied.

The total annual net production of gastropods was 5.336 g/m² by planimetry and 4.964 g/m² by equation (12) with an average value of 5.150 g/m². This is equivalent to 21,949 g cal/m², assuming a value of 4,262 g cal/g dry weight of mollusc tissue [obtained by averaging values reported by Golley (1961) and Paine (1965)]. The average net production of *Pisidium* was 2.815 g/m², or 11,998 g cal/m². If 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 *P. compressum*, total annual assimilation of the gastropod populations was 87,796 g cal/m², and that of the *Pisidium* population was 25,527 g cal/m² (total: 113,323 g cal/m²). This value for total gastropod assimilation is equivalent to 21.41 g/m² of plant material, assuming a calorie content of 4,100 g cal/g dry weight of plants. If 50% of material ingested is assimilated, about 43 g/m² of plant material was consumed. Plants were collected along with molluscs in the same samples and dry weights were estimated (exclusive of roots). The standing crop of *Potamogeton* spp. increased from 86.6 g/m² in April 1965 to 276.0 g/m² in August 1965, so that the minimum net production of plant material was 183.4 g/m². If the probable amount consumed by gastropods is added, the actual growth must have exceeded 226 g/m². Thus the gastropods, if they fed exclusively on *Potamogeton*, assimilated approximately 10% of the available net primary production or somewhat more if a lower calorific equivalent is assumed for the plant material.

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