Population studies of four species of mollusks in the Madison River, Yellowstone National Park
by David Miller Gillespie

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Zoology
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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 Nt = ln N0 + d/g (ln Q0 - ln Qt), where N0 and Nt are population numbers at initial and later times of observation, Q0 and Qt 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 (Pn) was then calculated by the equation: Pn = N0 Q0^k (l-k)^-1 (qt^l-k - Qo^l-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 areas, 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.

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Head, Major Department

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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

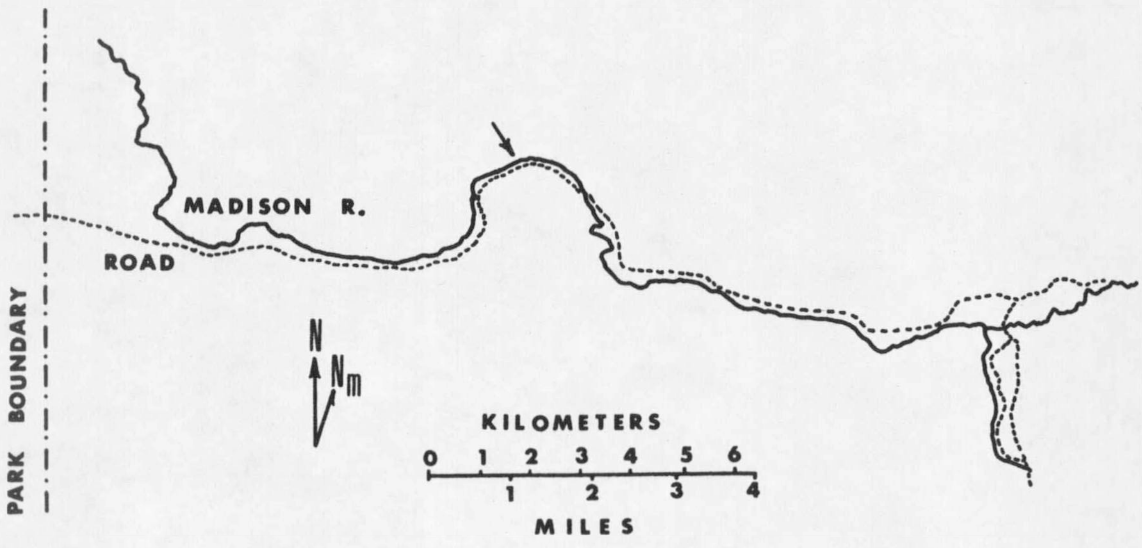

Figure 1. Madison River, Yellowstone National Park, showing study area (arrow).

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

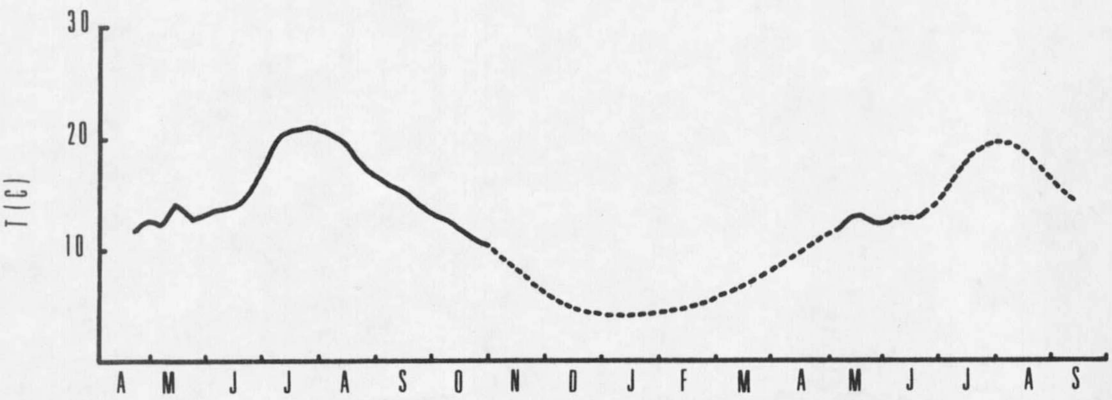

Figure 2. Average temperatures in Madison River April, 1964, to September, 1965. Solid line - thermograph data furnished by J. C. Wright. Dotted line estimated from maximum-minimum and pocket thermometer data.

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