J. Moll. Stud. (1987), **53**, 171–177. © *The Malacological Society of London 1987*

GROWTH AND DEMOGRAPHY OF POPULATIONS OF *BIOMPHALARIA PFEIFFERI* (GASTROPODA, PLANORBIDAE) IN THE LABORATORY

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(Received 10 November 1986)

ABSTRACT

The growth and demography of the freshwater snail *Biomphalaria pfeifferi*, an intermediate host of the parasitic worm *Schistosoma mansoni* in Eastern Zaïre, were investigated in the laboratory under two conditions of crowding. Both individual and population growth were depressed by crowding. Crowding reduced growth rate and all the variables and parameters related to reproduction (fecundity, instantaneous birth rate, net reproduction rate), but did not affect maximum size, survivorship, instantaneous death rate and life expectancy. The mechanism involved in these effects is likely to be exploitation competition for especially profitable food items such as diatoms.

INTRODUCTION

The freshwater snail *Biomphalaria pfeifferi* Krauss (Gastropoda, Planorbidae) is one of the obligate intermediate hosts of *Schistosoma mansoni*, a parasitic worm causing bilharziasis (schistosomiasis) in Zaïre. Bilharziasis is highly endemic in the Ruzizi plain (between longitudes 29° and 30°E. and latitudes 3° and 4°S.). Efficient efforts to control this disease are conditional on a thorough knowledge of the ecology and population dynamics of the host snail.

Several studies on the population dynamics of *Biomphalaria pfeifferi* have been carried out in the laboratory, focusing on the effects of temperature and calcium concentration on some demographic parameters (Sturrock, 1966; Shiff & Garnett, 1967; Williams, 1970; Harrison *et al.*, 1970; Nduku & Harrison, 1976; de Kock & van Eeden, 1981). On the other hand, to our knowledge there has been no investigation on the effects of population density on growth or demography of *Biomphalaria pfeifferi*, while these are relatively well documented in other *Bulinus* and *Biomphalaria* species (Chernin & Michelson, 1957a,b; Shiff, 1964; Jobin & Michelson, 1967; Simões *et al.*, 1974; Thomas & Benjamin, 1974). Also we do not know of any detailed field investigation on the population dynamics of *Biomphalaria pfeifferi*.

The aim of this project was to carry out a general study on the population dynamics of *Biomphalaria pfeifferi* in Eastern Zaïre, both in the field and in the laboratory. The present paper describes the growth and demography of cohorts reared in the laboratory at Lwiro (long. 28°48′E., lat. 2°15′S., altitude 1740 m), and compares crowded and uncrowded populations in order to investigate which aspects are affected by population density. The population dynamics in the field will be analysed in another paper (Loreau & Baluku, 1987).

MATERIAL AND METHODS

Rearing conditions

All rearings were performed in glass aquaria kept in a lighted and aerated place in the laboratory. The water used was the tap water of the laboratory, which is impounded from a near spring and treated by addition of lime. Its total hardness is 4.12 milliequivalents/l (corresponding to 50–70 mg/l of calcium approximately). Snails were reared at room temperature. Temperature was recorded daily both in the air and in the water; air temperature fluctuated between 21°C and 26°C with an average of 23.7°C, and water temperature fluctuated between 18.5°C and 24°C with an average of 21.8°C.

In order to start the cohorts, 90 adult snails were first caught in the Virunga stream, close to the laboratory. They were distributed into three groups of 30 individuals, which were placed in 55 × 28 × 37 cm aquaria filled with 20 l water. Each group was provided with 10 fresh leaves of *Rorippa aquatica* L. as food, and 10 stems of *Eichornia* sp. 30 cm long and 3 cm in diameter

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as laying support. Both plants are commonly found in the field and used by *Biomphalaria pfeifferi*. Although *Biomphalaria pfeifferi* lay eggs on *Rorippa* leaves and on the panes of aquaria as well, *Eichornia* stems were used because they are one of their preferred laying supports and can be easily handled later. The snails started laying eggs after two days. When covered with egg masses, *Eichornia* stems were cut up in three and placed in 12 × 12 × 6 cm jars filled with 300 ml water. Newly hatched snails were collected daily to constitute the cohorts. Ten groups of respectively 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100 eggs were also kept separately in identical jars to obtain data on hatching success.

Two cohorts of 30 individuals (uncrowded) and two cohorts of 300 individuals (crowded) were reared under the same conditions in 25 × 15 × 10 cm aquaria filled with 3.5 l water, and followed over almost one year, from March 1984 to February 1985. Every week, the water was changed, two *Rorippa* fresh leaves were provided in each aquarium (which represents an amount of food slightly in excess of the requirements of crowded cohorts), snails and fertile as well as non-fertile eggs were counted, and, for 10 snails per cohort, the maximum diameter of the shell was measured under a binocular to the nearest micrometric graduation (0.14 mm).

Growth curve

The maximum diameter of the shell was used as growth variable of *Biomphalaria pfeifferi*. A good correlation was found with log weight ($r = 0.99$, 5 d.f., $P < 0.001$). von Bertalanffy's (1938) model, which is in current use for the biometry of animals with a continuous growth, was fitted to the observed curves to get a predictive model of growth. It is given by the equation:

$$L_x = L_{\max}\,[1 - e^{-K(x - x_0)}]$$

where L_x is the size (here, the maximum diameter of the shell) at age x,
$L_{\max}$, the asymptotical maximum size,
K, a constant characteristic of growth rate,
x_0, the time prior to the origin when the size was zero (here: minus the duration of the egg stage).

K and $L_{\max}$ are determined by the slope and intercept on the x-axis of the regression line of growth rate on size.

Demographic variables and parameters

Demographic variables and parameters were estimated from the standard formulae for a stable age distribution (Pielou, 1977; Vandermeer, 1979). As the species is hermaphrodite, the calculations are simplified by the fact that the whole adult population can be considered as female.

(1) *Survivorship*
The survivorship at age x is given by $l_x = N_x/N_0$, where N_0 is the number of newborn individuals, and N_x, the number of individuals still alive at time x.

As the cohorts were initiated with hatchlings while birth should be considered to occur at egg laying, the age $x = 0$ was reset to the time of egg laying using the known duration of the egg stage, and the number N_0—here, the number of fertile eggs laid—was extrapolated from the number of hatchlings, N_h (h being the age at hatching), using the data on the hatching success, N_h/N_0.

(2) *Fecundity*
The age-specific mean fecundity in the age class (x, $x + 1$) was approximated by $m_{x'} = G_{x+1}/N_{x'}$, where G_{x+1} is the number of fertile eggs collected at time $x + 1$ (i.e., laid between x and $x + 1$), and $N_{x'} = (N_x + N_{x+1})/2$ is the approximated number of individuals at age $x' = x + 1/2$. This assumes that all births occur at the midpoint of the age class.

(3) *Net reproduction rate*
The net reproduction rate is given by $R_0 = \int_0^\infty l_x m_x dx$, which was calculated as:

$$R_0 = \sum l_{x'} m_{x'} = \sum (N_{x'}/N_0)(G_{x+1}/N_{x'})$$
$$= \sum G_x/N_0$$

(4) *Intrinsic rate of natural increase*
The intrinsic rate of natural increase, r, is obtained by solving Lotka's equation for a stable age distribution:

$$\int_0^\infty l_x m_x e^{-rx} dx = 1$$

This was approximated by:

$$\sum G_{x+1} e^{-rx'}/N_0 = 1$$

and the equation was solved by iterations using a computer.

(5) *Instantaneous birth and death rates*
The instantaneous birth rate is given by $b = l/\int_0^\infty l_x e^{-rx} dx$. It was approximated by $b = N_0/\Sigma N_{x'} e^{-rx'}$.

The instantaneous death rate is then simply $d = b - r$.

(6) *Mean generation time*
The mean generation time is given by $T = \ln R_0/r$.

(7) *Life expectancy*
The life expectancy of an individual aged x is given by $e_x = \int_x^\infty l_x dx/l_x$. For later comparison with field data, two values were of special interest here: the life expectancy at laying, e_0, and the life expectancy at hatching, e_h. By linear approximation of the integral $\int_x^\infty l_x dx$, they were calculated as:

$$e_0 = 0.5 + \sum_{x=1}^{\infty} N_x/N_0$$

$$\text{and } e_h = 0.5 + \sum_{x=h+1}^{\infty} N_x/N_h.$$

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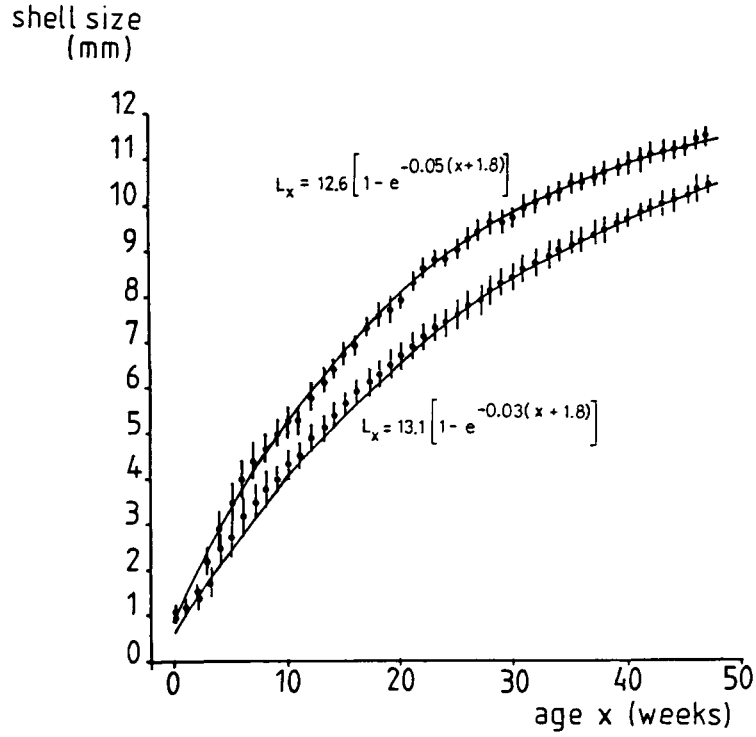


Fig. 1. Growth curves of uncrowded (above) and crowded (below) populations. Observed weekly means (dots) with 95% confidence intervals (vertical lines), and curves predicted by von Bertalanffy's equations.

RESULTS

Egg development

Hatching occurred 12 to 13 days after laying. Hatching success was fairly constant, with a weighted mean of 81.5% and a standard deviation of 1.5%. This mean value was used to calculate the numbers of fertile eggs originally in the cohorts, N_0.

Growth

Fig. 1 shows the growth curves of the snails under the two experimental conditions. von Bertalanffy's equations fitted both of them very well. Growth was markedly depressed by crowding, mean shell sizes being significantly different from the 5th week onwards (t-test, $P < 0.05$). Crowding affected growth rate, but it did not decrease the estimated maximum shell size.

Survivorship

The survivorship curves for the four experimental cohorts are shown in Fig. 2. No clear differences appeared between crowded and uncrowded cohorts, but the former seemed to survive better in the long run (after 46 weeks). Thus crowding had at most a weak effect on mortality, and this effect was rather in the direction of decreasing mortality.

Note the symmetric sigmoidal shape of the curves, which does not correspond to Slobodkin's (1962) classical types.

Fecundity

The fecundity curves are shown in Fig. 3. They almost coincide for cohorts under the same conditions of crowding, whereas curves of cohorts under different conditions are completely separated. Crowding reduced fecundity by more

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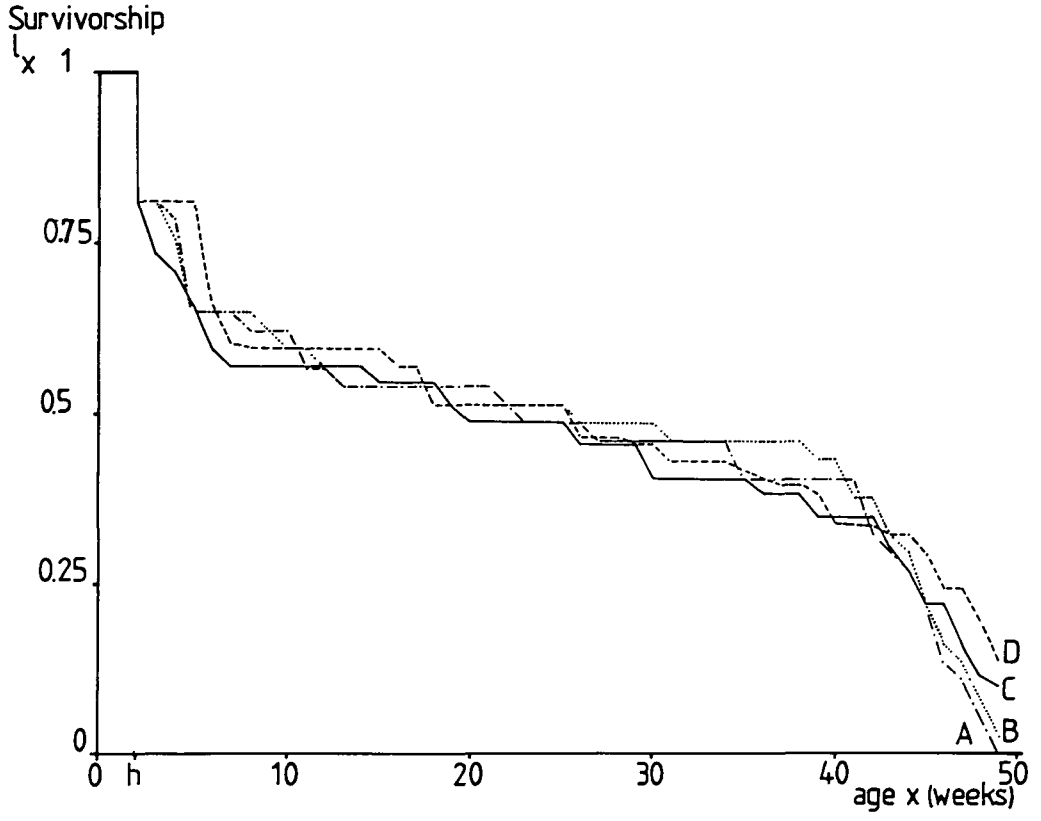


Fig. 2. Survivorship curves of the uncrowded (A and B) and crowded (C and D) cohorts. *h* is the age at hatching (1.8 weeks).

than half, although it did not alter the general shape of the curve: all cohorts started laying eggs 13 weeks after hatching and reached a maximum fecundity 8 weeks later. However, the fecundity of the crowded snails declined less sharply after the peak.

Demographic parameters

Table 1 shows the values of the demographic parameters for the four cohorts. The synthetic parameter *r* was virtually identical in the cohorts under the same conditions of crowding, but was very sensitive to crowding. Although only two replicates were available under each experimental condition, the decrease of *r* with crowding was very highly significant. Of the two components of the intrinsic rate of natural increase, only the birth rate was affected by crowding, while the death rate was not. Also, there was a highly significant reduction in the net reproduction rate, but no significant effect on life expectancies. Lastly, crowding tended to lengthen the mean generation time, though this result was not significant.

DISCUSSION

A quantitative comparison of the present results with other data on the growth and demography of *Biomphalaria pfeifferi* is very difficult. Among the scarce literature on the subject, Shiff & Garnett's (1967) study was disturbed by 'atypical' migratory behaviours, while Sturrock (1966), Williams (1970), Harrison *et al.* (1970) and de Kock & van Eeden (1981) do not seem to have calculated demographic parameters properly, for they seem to have started their cohorts several weeks after egg laying. This of course eliminates the high mortality in the early life and shortens the generation time, both

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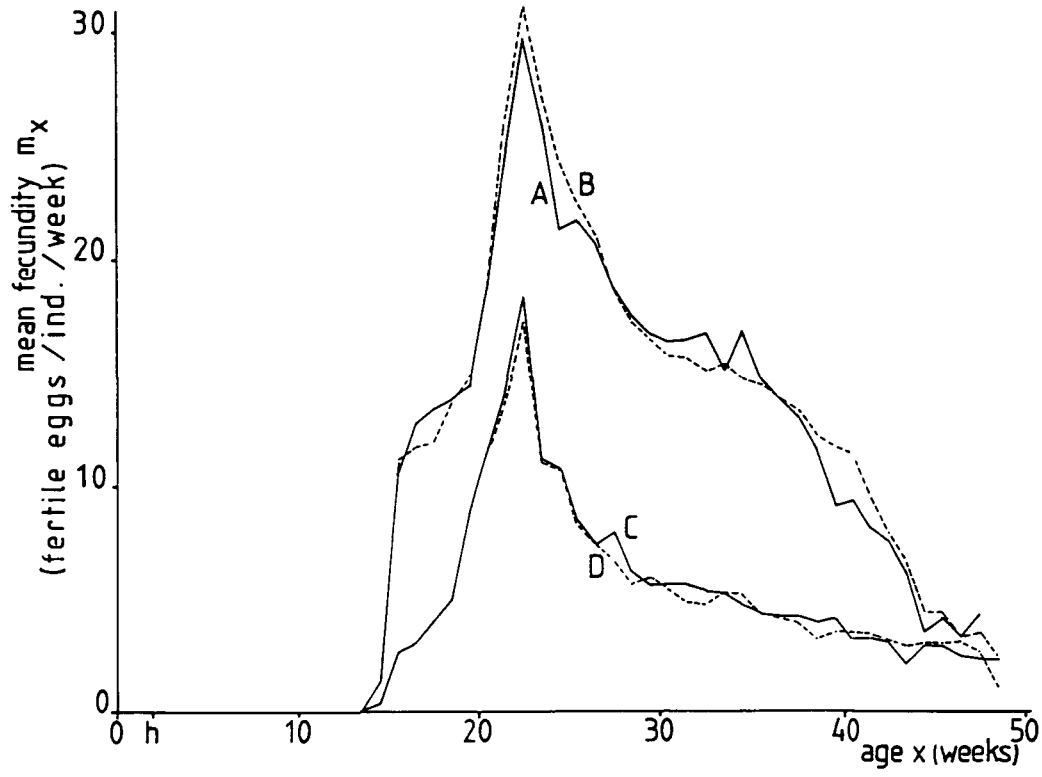


Fig. 3. Fecundity curves of the uncrowded (A and B) and crowded (C and D) cohorts.

effects contributing to overestimated r values. It may also explain why the symmetric sigmoidal shape of survivorship curves did not appear in other laboratory studies; this combination of higher mortality in very young and very old snails was found by Barlow & Muench (1951) and O'Keeffe (1985) in other snail species. Furthermore, experimental conditions have differed widely among studies. The conditions in the present study were suboptimal, both regarding temperature (lower than the optimum around 25–29°C: Sturrock, 1966; Shiff & Garnett, 1967; de Kock & van Eeden, 1981), hardness (higher than the optimum around 12 mg Ca^{++}/l: Williams, 1970, Harrison *et al.*, 1970), food (inferior to the widely used lettuce: Frank, 1963; Thomas *et al.*, 1983), and perhaps crowding (even our uncrowded populations were denser than in the other studies—but see Thomas & Benjamin, 1974, for the possibility of an Allee effect at lower densities).

Taking all those factors into account, it would seem that the demographic characteristics of our populations were consistent with Harrison *et al.*'s (1970) data, as well as Shiff & Garnett's (1967) data for their cohort reared at room temperature. The exceptionally high r values in de Kock & van Eeden (1981) were probably due to the artificial food on which the snails were fed. We should expect, however, that more precise comparisons between populations would reveal genetic differences in growth and demography. This is suggested e.g. by Harrison *et al.*'s (1970) data, which show that fecundity of snails from different biotopes tended to be higher under experimental conditions of hardness that were similar to those encountered by the snails in their biotope.

Crowding proves to have marked effects on growth and demography of *Biomphalaria pfeifferi*—both individual and population growth are depressed by crowding. But the effects are very specific. Crowding affects growth speed and all the aspects or parameters related to reproduction: fecundity, birth rate, net reproduction rate. On the other hand, it does not seem to affect maximum size and all the aspects or parameters related to mortality: survivorship, death

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Table 1. Demographic parameters for the 4 cohorts (time unit = 1 week), and t-tests on the difference between the means of crowded and uncrowded populations (2 d.f.).

		uncrowded		crowded		t-tests	
		A	B	C	D		
Intrinsic rate of natural increase	r	0.2366	0.2359	0.1910	0.1917	t = 91.82,	P < 0.001
Instantaneous birth rate	b	0.2977	0.2976	0.2575	0.2448	t = 7.34,	P < 0.05
Instantaneous death rate	d	0.0611	0.0617	0.0665	0.0531	t = 0.23,	0.8 < P < 1
Net reproduction rate	R_0	216.6	226.8	86.0	87.4	t = 26.18,	P < 0.01
Mean generation time	T	22.73	22.99	23.32	23.32	t = 3.59,	0.05 < P < 0.1
Life expectancy at laying	e_0	24.09	24.66	23.43	24.85	t = 0.32,	0.6 < P < 0.8
Life expectancy at hatching	e_h	27.37	28.07	26.40	28.14	t = 0.48,	0.6 < P < 0.8

rate, life expectancies. Similar effects on growth and fecundity have already been documented in other freshwater snail species (Chernin & Michelson, 1957a; Shiff, 1964b; Jobin & Michelson, 1967; Simões *et al.*, 1974), but only a few authors reported the simultaneous lack of effect on mortality (Eisenberg, 1966; Thomas & Benjamin, 1974).

The mechanism involved in the negative intraspecific density-dependent effects on individual and population growth is most likely exploitation competition for food, as stressed by other authors (Eisenberg, 1966; Jobin & Michelson, 1967), though competition may also occur through direct interference, due e.g. to mucus marks or accumulation of metabolic waste. Other chemical alterations of the medium under conditions of crowding, such as depletion of dissolved oxygen and calcium, cannot be excluded, but they seem unlikely in the present study, when the aquaria were kept in an aerated place and the calcium concentration was above the optimum. For it to have an effect, competition for food does not require a complete depletion of food resources. Thomas *et al.* (1983) showed that relative food shortage is sufficient for the negative effects of competition to be felt on the growth of *Biomphalaria glabrata*. One of the ways this relative food shortage can be produced is through the limitation of the most profitable food items. This mechanism is quite likely since *Biomphalaria pfeifferi* in the field proved to feed, not on the plants themselves which are used in the laboratory rearings, but on diatoms which grow on them (Baluku, in prep.). It would then provide the explanation for the specificity of the effects of crowding: the shortage of especially profitable food items such as diatoms can slacken growth and reproduction, but will not increase mortality as long as alternative food is available.

ACKNOWLEDGEMENTS

We wish to thank G. Josens, who suggested this work and read the manuscript. Our thanks to C. Foccroulle for preparing the figures. The first author acknowledges a grant as senior research assistant of the National Fund for Scientific Research (Belgium).

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