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POPULATION DYNAMICS OF THE FRESHWATER SNAIL *BIOMPHALARIA PFEIFFERI* IN EASTERN ZAÏRE

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ABSTRACT

The population dynamics of the freshwater snail *Biomphalaria pfeifferi*, an intermediate host of the parasitic worm *Schistosoma mansoni*, was studied in the Virunga stream in Eastern Zaïre.

Methods are developed to estimate age-specific survivorship from regular quadrat-sampling data without assuming a constant mortality rate, and to approximate age-specific fecundity when the fecundity function is known in the laboratory.

The population dynamics in the field was found to be very different from that in the laboratory: it is basically discontinuous, with one main generation per year; a massive mortality occurs after hatching; fecundity is reduced considerably; and there are marked seasonal variations in both survivorship and fecundity. Time-dependent demographic parameters were estimated by month instead of by cohort. They show that the environmental conditions are favourable to an increase of the population only during a short period of the year. The intrinsic rate of natural increase, r, was found to be well correlated with the changes in egg density.

The environmental factors determining the population dynamics in the Virunga are discussed; current speed seems critical.

INTRODUCTION

In a previous paper (Loreau & Baluku, 1987), we described a laboratory study on the growth and demography of *Biomphalaria pfeifferi* (Krauss), an intermediate host of the parasitic worm *Schistosoma mansoni* in Eastern Zaïre. In this paper, we now turn to the population dynamics of *Biomphalaria pfeifferi* in the field, i.e. the Virunga stream at Lwiro (longitude 28°48′E., latitude 2°15′S., altitude 1740 m), close to the laboratory. While several field studies have been carried out on the population dynamics of other schistosome host snails, such as *Oncomelania quadrasi* (Pesigan *et al.*, 1958), *Bulinus* species (Webbe, 1962; Shiff, 1964c; Dazo *et al.*, 1966; O'Keeffe, 1985a, b) and *Biomphalaria glabrata* (Sturrock, 1973a, b), to our knowledge there has been no quantitative demographic analysis of the population dynamics of *Biomphalaria pfeifferi*. Yet this is a prerequisite to any attempt to control the transmission of bilharziasis through the host snail.

Because field populations are not small isolated cohorts under relatively constant conditions as they are in the laboratory, but large complex entities in a fluctuating environment, the analysis of their dynamics is more difficult to achieve and requires several approximations. Field studies on the population dynamics of other schistosome host snails have generally resorted to simplifying assumptions, such as constant mortality rates (Pesigan *et al.*, 1958; Webbe, 1962, 1965a; Dazo *et al.*, 1966; Sturrock, 1973a). An alternative approach was followed by O'Keeffe (1985a, b), who used more sophisticated field methods such as trapping, mark-recapture and enclosing of populations in boxes. However, when only data from regular sampling are available, it is still possible to carry out a detailed analysis relaxing some simplifying assumptions, on the basis of standard equations of population dynamics. We shall present and apply here a method of analysis along that line which utilizes data gathered in the laboratory, developing some procedures used by Shiff (1964c).

A special emphasis will be on comparing laboratory and field results, because they might reveal important differences and yet such comparisons have been attempted very rarely (Shiff, 1964a, b, c). The possible environmental factors that determine the population dynamics in the field will be discussed in the light of that comparison.

STUDY SITES AND FIELD METHODS

The study sites and the sampling methods have been described extensively in Baluku and Josens (in prep.). Two biotopes (no. 4 and 5) contained *Biomphalaria pfeifferi* and are considered here. Figure 11 summarizes the main characteristics of biotope 4 during the periods studied.

Quadrat sampling was performed using a wooden frame 25 × 25 cm and 30 cm high. The material collected within the frame was washed on a sieve with 0.8 mm mesh, eggs and snails were sorted out on the spot, preserved in 70° alcohol and later counted and measured in the laboratory. 15 samples were taken in each biotope every 24th of the month from July 1982 to March 1983 and from March 1984 to January 1985. In 1984–85, however, after a disturbance of biotope 5, the local population was virtually extinct; the results for that year will therefore include only biotope 4. Using marked individuals, the mean sampling efficiency was found to be 72% for *Biomphalaria pfeifferi*.

MATHEMATICAL ANALYSIS OF DATA

Basic principle

Since data are presented in the form of size distributions gathered at regular monthly intervals, a model expressing the change in the number of individuals of a given size from one month to the next is needed in order to obtain variables that are of interest to population dynamics. Models based directly on size classes are conceivable (Lynch, 1983; Kirkpatrick, 1984), but are needlessly complicated when one is not particularly concerned in a size-specific demography. Therefore the first step consists in equating size to age. To that effect, as Shiff (1964c) did, we shall use von Bertalanffy's equation which was obtained in the laboratory, assuming that it is approximately valid in the field—this will be checked later. Thus the sizes corresponding to the limits of monthly age classes can be calculated, and the data converted into age distributions. The class interval is of course chosen equal to the interval between the field censuses. The relation between class frequencies from one census to the next is then straightforward:

$$N_{x+1,t+1} = P_{x+1} N_{x,t} \qquad (1)$$

which is the basic equation for population projection matrices (Pielou, 1977; Vandermeer, 1979).

$N_{x,t}$ is the number of individuals in the age class $(x, x+1)$ at month t,

$N_{x+1,t+1}$, the number of individuals in the next age class a month later, and

P_{x+1}, the "transition probability" from the age class $(x, x+1)$ to the class $(x+1, x+2)$. Note that the transition probabilities can be allowed to vary in time as well. Equation (1) allows them to be estimated from the known $N_{x,t}$.

Survivorship

The transition probabilities are related to the survivorship function l_x by (Pielou, 1977; Vandermeer, 1979):

$$P_x = \frac{\int_x^{x+1} l_x \mathrm{d}x}{\int_{x-1}^{x} l_x \mathrm{d}x} \qquad (2)$$

Note that this equation is not strictly true because it assumes implicitly that births did not vary during the time unit when the cohort was formed. However, when the P_x are calculated from data over a whole reproduction cycle, the variations in births will cancel each other out.

Since the form of the survivorship function is unknown in equation (2), this has to be approximated by:

$$P_x = \frac{l_x + l_{x+1}}{l_{x-1} + l_x} \qquad (3)$$

If $n+1$ is the number of age classes, there are n such equations. Because $l_0 = 1$ and $l_{n+1} = 0$, the system of n equations can be solved for the n unknowns, the l_x for x from 1 to n.

We now have to consider the problem of the egg stage, which must constitute the first class but only lasts 0.4 month (Loreau & Baluku, 1987). To calculate the transition probability from the egg stage to the class of snails aged 0 to 1 month, we shall have to extrapolate the number of eggs produced in a month. The way to do it is detailed in the next section, but let us specify from now on, to avoid confusion, that the age $x = 0$ will be redefined as the hatching time of snails, and $n+1$ as the number of age classes after hatching. Assigning eggs to a separate age class is biologically justified and simplifies the solution of (3), for we can assume that mortality is negligible during the egg stage. Eisenberg (1966) did not detect egg mortality for *Lymnaea elodes* in the field, and this assumption is at any rate preferable to the assumption of a linear decrease in survivorship which underlies equation (3), because hatching is always accompanied by a sudden loss of part of the population (see e.g. the survivorship curves in Loreau & Baluku, 1987). Its consequences are further discussed later.

With this assumption, the integral in the denominator of equation (2) is equal to 1 for P_0, and the first equation in system (3) reduces to:

$$P_0 = (l_0 + l_1)/2$$

where l_0 is the survivorship immediately after hatching. This equation can be rewritten as

$$l_0 = 2P_0 - l_1$$

Replacing l_0 by this expression in equation (3) for P_1, and repeating for the successive l_x, we get the system of equations:

$$\begin{cases} l_0 = 2P_0 - l_1 \\ l_1 = 2P_0P_1 - l_2 \\ \vdots \\ l_x = 2\prod_{y=0}^{x} P_y - l_{x+1} \\ \vdots \\ l_n = 2\prod_{y=0}^{n} P_y \end{cases} \quad (4)$$

Replacing now the l_{x+1} by their expressions backwards provides the explicit solutions:

$$l_x = 2\sum_{z=x}^{n} (-1)^{z-x} \prod_{y=0}^{z} P_y \quad (0 \leqslant x \leqslant n) \quad (5)$$

Using equation (5) the whole survivorship curve can be constructed. However, the method has two limitations. First, data are needed over the entire life span for any l_x to be calculated, which may not always be possible in practice. Second, the linear approximations in (3) impose constraints on P_x values. when these are not respected by actual data, oscillations will appear in the successive l_x values. The necessary monotonic decrease of the survivorship curve imposes, for all x:

$$l_{x-1} \geqslant l_x$$

which becomes in system (4):

$$\prod_{y=0}^{x-1} P_y \geqslant l_x$$

or, using (5):

$$0.5 \geqslant \sum_{z=x}^{n} (-1)^{z-x} \prod_{y=x}^{z} P_y$$

Qualitatively, this condition means that there cannot be too abrupt a decrease in successive P_x values.

When required by the data, an alternative to equation (5) is to approximate survivorship at the midpoints x' of the age classes $(x, x+1)$:

$$l_{x'} = (l_x + l_{x+1})/2$$

which, using (4), reduces to:

$$l_{x'} = \prod_{y=0}^{x} P_y \quad (6)$$

or, when a particular cohort is followed, simply to:

$$l_{x'} = N_x/N_e$$

where N_e is the number of eggs at the origin of the cohort. This simple expression avoids both above-mentioned limitations.

Monthly egg production

To find the transition probability P_0 from the egg stage to the first age class of snails, we must estimate $N_{e,t-1}$, the number of fertile eggs produced in a month that originated the $N_{0,t}$ snails aged 0 to 1 month in each census. Again assuming no mortality during the egg stage, this number is equal to G_{t-1}, the number of fertile eggs present in the last census, plus G'_{t-1}, the number of fertile eggs laid between $t-1$ and $t-h$ (h being the duration—shorter than one month—of the egg development). By linear approximation of egg production between censuses, G'_{t-1} is estimated by the mean egg production per time unit between $t-1$ and $t-h$, $(G_{t-1} + G_t)/2h$, times the time interval, $1-h$. Thus:

$$G'_{t-1} = (G_{t-1} + G_t)(1-h)/2h$$

The required monthly egg production is then:

$$\begin{aligned} N_{e,t-1} &= G_{t-1} + G'_{t-1} \\ &= [(1+h)G_{t-1} + (1-h)G_t]/2h \end{aligned} \quad (7)$$

Grouping of age classes

A last problem arises when numbers in classes with low frequencies are affected by random variations, in particular in the last age classes. Then transition probability estimates may take on impossible values greater than 1. A way to cope with this problem is to group some age classes and to make some simplifying assumptions within the group, i.e. that the class frequencies are randomly distributed and best estimated by the mean class frequency, and that the transition probabilities are equal.

Let d_z be the number of classes in the group z, and P_z the transition probability to each class

in the group. Then the total frequency of the group at time $t + 1$, $N_{z,t+1}$, will be equal to the number of individuals coming from the last class in the previous group at time t, $P_z N_{z-1,t}/d_{z-1}$, plus the number of individuals surviving from the first $d_z - 1$ classes in the group, $(d_z - 1)P_z N_{z,t}/d_z$. Model (1) is thus replaced by:

$$N_{z,t+1} = P_z[N_{z-1,t}/d_{z-1} + (d_z - 1)N_{z,t}/d_z] \quad (8)$$

It is readily verified that when groups are reduced to single classes (i.e. $d_z = 1$ for all z), model (1) is recovered.

Life expectancy

As in the laboratory, life expectancies are estimated at laying (e_l) and at hatching (e_h). They are calculated by linear approximation of the integral of the survivorship function after hatching:

$$e_l = h + \sum l_{x'} \quad (9)$$

$$e_h = \sum l_{x'}/l_0 \quad (10)$$

where $l_{x'}$ is the survivorship at the midpoint of the class $(x, x + 1)$, and is obtained directly when equation (6) is applied, or by a mean value when equation (5) is applied.

Age-specific fecundity

Since no direct data on age-specific fecundity in the field are available, this will be approximated using an indirect method inspired by Shiff (1964c), which we shall present in a more elaborate and formal way.

The total egg production per time unit at time t can be estimated by G_t/h, where, as before, G_t is the number of fertile eggs censused at time t, and h is the duration of the egg stage, and thus the lapse of time over which the collected eggs were laid. Since it is equal to the sum of the productions of all age classes, we have:

$$\sum_x N_{x,t} m_{x,t} = G_t/h \quad (11)$$

where $m_{x,t}$ is the mean fecundity in the class $(x, x + 1)$.

Now we assume that the only factor that varies in time is the general level of egg production, but not the proportional reproductive potentials of the various age classes, which remain the same as in the laboratory, i.e.:

$$m_{x,t} = f_x M_t \quad (12)$$

where f_x is the constant proportion of eggs that can be produced by an individual in the age class $(x, x + 1)$, and M_t is the sum of the numbers of eggs produced per individual over all age classes at time t. M may be called the "maximum reproductive capacity", because it represents the total number of eggs that the individual with the longest life span would produce in its lifetime (under the conditions prevailing at time t). It thus has an interest on its own, as a measure of the favourableness of the environment for reproduction. f_x is determined by applying equation (12) to the fecundity curve obtained in the laboratory:

$$f_x = \frac{\int_x^{x+1} m_x dx}{\int_0^{\infty} m_x dx} \quad (13)$$

Introducing (12) into (11) provides an estimate of M_t:

$$M_t = \frac{G_t}{h \sum N_{x,t} f_x} \quad (14)$$

which in turn can be introduced into (12) to get an estimate of $m_{x,t}$.

The hypothesis made in (12) is of course critical, and since there is no means to verify it here, the estimates must be considered as crude approximations.

Demographic parameters

Knowing the age-specific survivorship and fecundity, the standard demographic parameters can be estimated by linear approximations as in the laboratory.

The net reproduction rate is then calculated by:

$$R_0 = \sum l_{x'} m_{x'} \quad (15)$$

where x' is the midpoint of the age class $(x, x + 1)$, and $m_{x'}$ is taken as equal to m_x, assuming linearity of the fecundity function within each age class.

The intrinsic rate of natural increase, r, is obtained by iterative solution of:

$$\sum l_{x'} m_{x'} e^{-rx'} = 1 \quad (16)$$

The instantaneous birth rate is calculated by:

$$b = [(1 - e^{-rh})/r + l_{x'} e^{-rx'}]^{-1} \quad (17)$$

The first term in the square brackets corresponds

to the integral

$$\int_0^h l_x e^{-rx} dx$$

over the egg stage, with $l_x = 1$.

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

In all these calculations, the age $x = 0$ is of course reset to the time of laying.

RESULTS

Discontinuity of population dynamics

The fluctuations in snail and egg densities over the two years 1982 and 1984 are shown in Fig. 1. Changes were similar in snails and in eggs during the two years. They clearly point out the existence of a yearly cycle in density, which reaches a maximum in June, at the beginning of the dry season, and a minimum around January, in the middle of the rainy season.

Seasonality is an essential feature determining the population dynamics of *Biomphalaria pfeifferi* in the field by introducing discontinuity in it. Although continuity does exist to some degree by the fact that reproduction never stops, the population structure is very heterogeneous and dominated by a few successive cohorts. This is illustrated in Fig. 2 by the changes in the size structure of the *Biomphalaria pfeifferi* population after the occurrence of the peak density in 1984. Frequency peaks, which must correspond to periodic bursts of breeding activity, were propagated regularly along the size axis from June to November.

Growth as compared to laboratory predictions

Figure 2 was constructed to test the adequacy of the predictions from von Bertalanffy's equation in the laboratory to account for the growth in the field. This is of course a qualitative test because the precise growth curve is expected to vary in time, as shown for *Bulinus globosus* by O'Keeffe (1985a), and because quantitative data on size frequencies will be affected by sampling, population movements, etc. Nevertheless, von Bertalanffy's equation for uncrowded populations (Loreau & Baluku, 1987) appears to account reasonably well for the month-to-month movements of some regular frequency peaks (Fig. 2). The fit was also good in 1982; it is worth noting that an even better fit was found in another stream where frequencies were higher (Baluku and Loreau, in prep.). On the other hand, von Bertalanffy's equation for crowded populations was not able to predict peak movements. Thus growth in field populations seemed to be similar to that of uncrowded laboratory populations, and von Bertalanffy's equation for these was used in the later analysis.

Age structure, generation time and longevity

The changes in the age structure, as inferred from size frequencies using von Bertalanffy's equation, are shown in Fig. 3. The cohorts of snails born from May to July appear to predominate in the population until the following year, which means that, despite the continuous reproduction, there is one main generation per year. This contrasts with the laboratory popu-

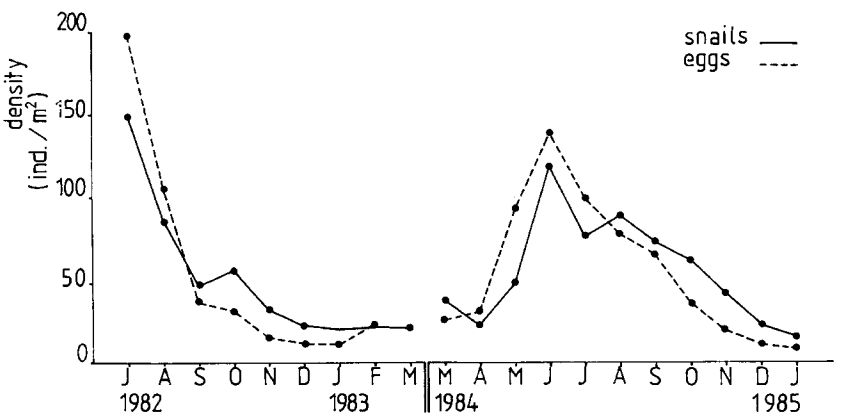


Fig. 1. Changes in egg and snail population densities over the periods studied (data uncorrected for sampling efficiency).

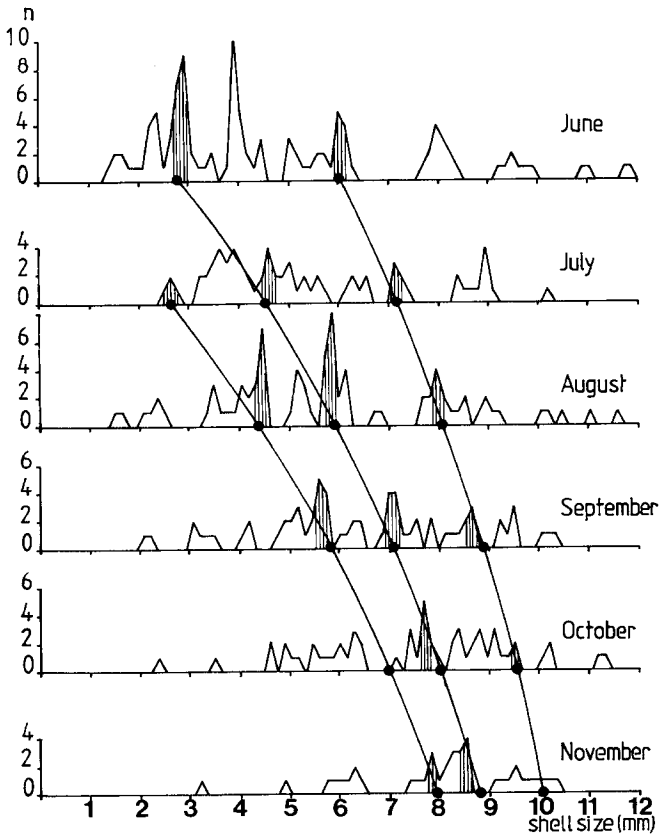


Fig. 2. Changes in the size structure from June to November 1984, and growth curves predicted by von Bertalanffy's equation for uncrowded laboratory populations, compared to the observed movements of a few frequency peaks (hatched). Shell size is the maximum diameter of the shell, measured to the nearest micrometric graduation (0.14 mm), and n is the number of individuals for each graduation.

lations, which have a mean generation time of 5.3 months and a maximum egg production after 5 months (Loreau & Baluku, 1987). Thus a powerful environmental factor must act to delay the main reproductive effort by half a year.

Longevity can be high in the field, since individuals of sizes corresponding to up to 19 months were found.

Survivorship and life expectancy

Because of the month-to-month fluctuations in class frequencies, detailed survivorship curves were only obtained from pooled data over a year. Transition probabilities were thus calculated as:

$$P_{x+1} = \frac{\sum_{t=2}^{k} N_{x+1,t}}{\sum_{t=1}^{k-1} N_{x,t}} \qquad (18)$$

in place of equation (1), k being the number of successive monthly censuses.

A problem arose from the under-representation of the first snail age class, which often had lower frequencies than the following one. This is most likely due to the undersampling of young snails, which are colourless and only slightly larger than the sieve's mesh. Therefore data for that class were discarded, and the first

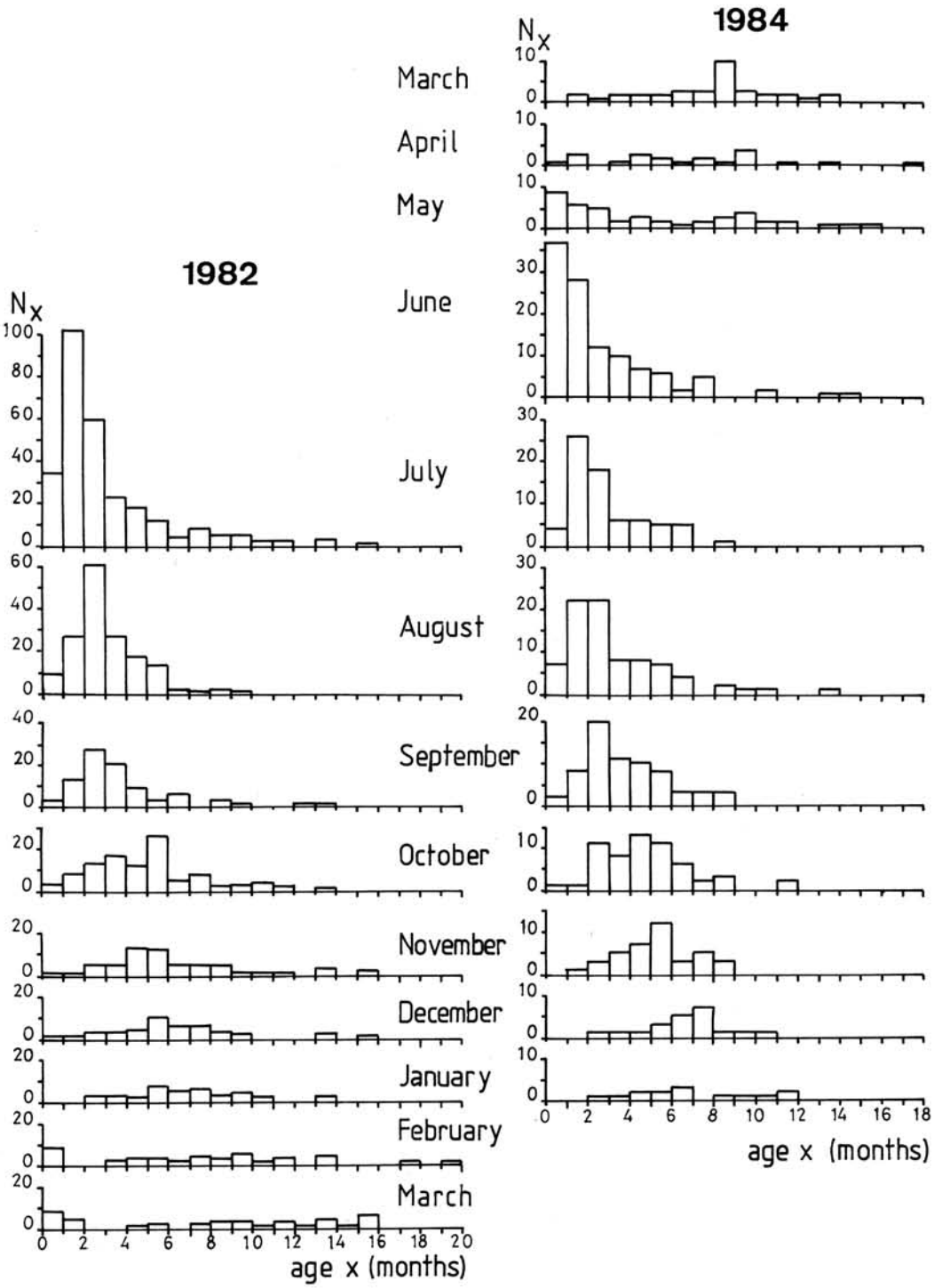


Fig. 3. Changes in the estimated age structure during the two years studied. N_x is the number of individuals per monthly age class.

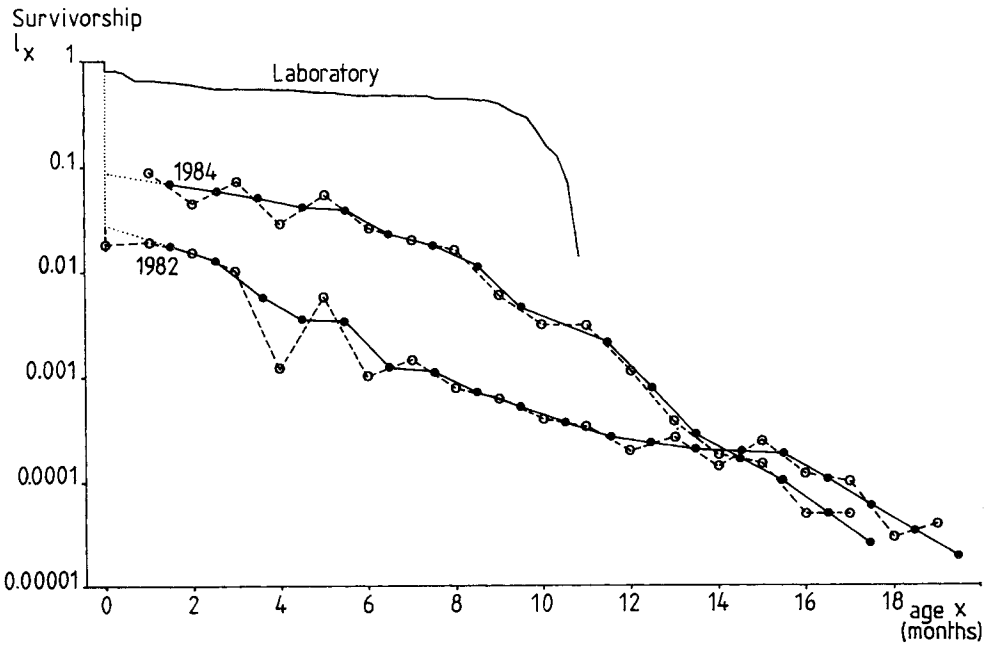


Fig. 4. Average survivorship curves in 1982 and 1984, compared to the mean curve for uncrowded populations in the laboratory (logarithmic scale). Dashed lines: survivorship estimated using equation (5); solid lines: survivorship estimated using equation (6), with extrapolation of l_0 (dotted lines). Classes were grouped over the following age intervals (in months): (9, 12), (12, 14), (14, 16) and (16, 20) in 1982; (2, 4), (10, 12), (14, 16) and (16, 18) in 1984. Model (8) was then applied.

two transition probabilities were replaced by a single one from the egg stage to the second snail class.

The average survivorship curves for 1982 and 1984 are shown in Fig. 4, and compared to the mean curve for uncrowded laboratory populations. Equation (5) turned out to produce oscillations, and thus equation (6) was also applied. Survivorship curves in the field are strikingly different from that in the laboratory. Whereas the latter has a symmetric sigmoidal shape (which becomes convex on the logarithmic scale of Fig. 4), the former combine a huge mortality after the hatching of snails and a more or less constant mortality rate later (producing a straight line on a logarithmic scale). Using this property, the curves were prolonged to the origin by a straight line having the same slope as that between the first two l_x estimates ($l_{1.5}$ and $l_{2.5}$) in order to extrapolate the survivorship after hatching, l_0. This amounted to only 2.7% in 1982 and 8.5% in 1984, i.e. values 10 to 30 times lower than the 81.5% in the laboratory.

Accordingly life expectancy at laying was very low: 2.0 weeks in 1982 and 3.5 weeks in 1984, i.e. an order of magnitude below the values of 23.4 to 24.8 weeks found in the laboratory. On the other hand, the discrepancies between the life expectancies at hatching were much smaller: 11.3 weeks in 1982 and 20.1 weeks in 1984, versus 26.4 to 28.1 weeks in the laboratory. This again stresses that the main difference between field and laboratory populations lies in the mortality of newly hatched snails.

Seasonal changes in survivorship and life expectancy

To investigate the seasonal changes in survivorship and life expectancy in spite of the fluctuations in successive class frequencies, survivorship curves for successive monthly cohorts were constructed very roughly by keeping only the highest decreasing class frequencies and replacing all frequencies inferior to a frequency that follows by the latter. This assumes that when some classes had lower frequencies than a following class, they were likely to be partly inaccessible to sampling, as will be discussed

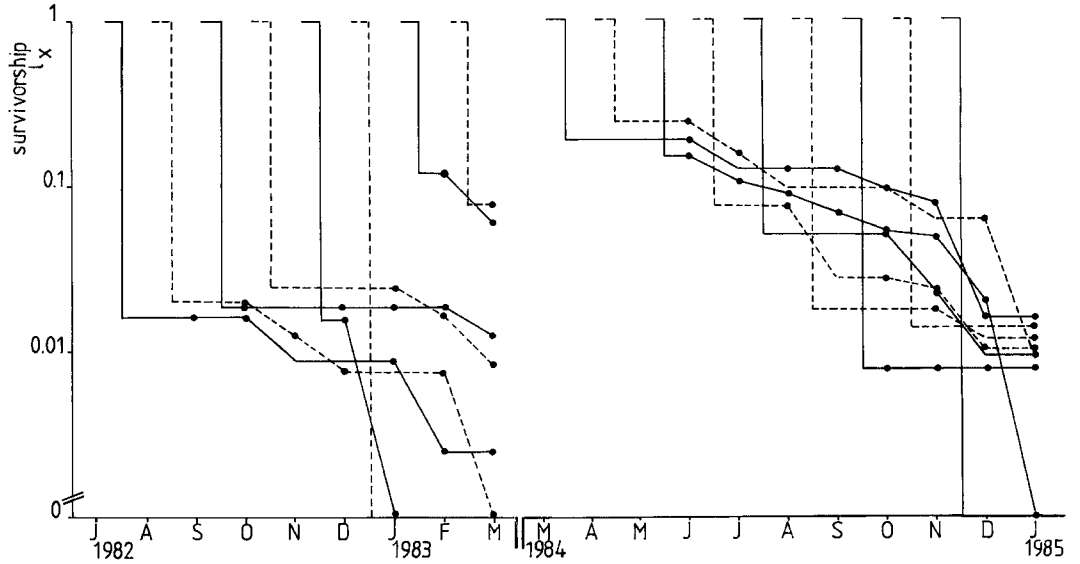


Fig. 5. Approximated survivorship curves of successive monthly cohorts in 1982 and 1984 (logarithmic scale). Dots correspond to the highest decreasing values which were kept to construct the curves.

later for the first age classes. Then equation (6) was applied. The results in Fig. 5 show that survivorship depends strongly on season, even more on season than on age since the cohorts born from March to October had roughly the same survivorship at the end of the year in 1984. Mortality at hatching is especially affected by those seasonal changes and seems to follow a yearly cycle, with a minimum in April and a steady increase until December. This appears clearly in the marked changes in the life expectancy at laying (Fig. 6). On the other hand, the

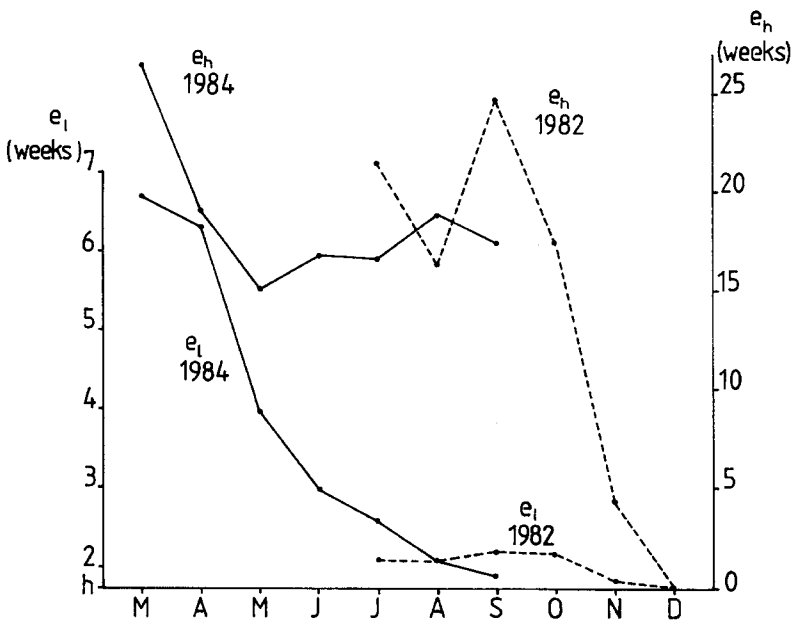


Fig. 6. Changes in the life expectancies estimated at laying (e_l) and at hatching (e_h) of cohorts born in the months indicated, in 1982 and 1984. The results are expressed in weeks for comparison with laboratory results.

life expectancy after hatching fluctuated less widely and more irregularly, except for a brutal drop in November–December, which shows that survivorship during most of the lifetime is not so much affected by season. Note that seasonal changes in survivorship were rather similar in 1982 and 1984, and thus the lower average survivorship in 1982 which appeared in Fig. 4 did not reflect a true difference between the population dynamics in the two years, but was mainly a result of the fact that the censuses in 1982 did not cover the period of lowest juvenile mortality. Therefore the curve for 1984 should be closer to the yearly average.

The corrected curves in Fig. 5 hide some fluctuations that are of interest. An inspection of Fig. 3 reveals that the peak density in June 1984 was accompanied by an increase in the frequencies of all the first age classes, which already starts in May. This cannot be attributed to chance: a t-test, after logarithmic transformation of the data to normalize the frequencies and stabilize the variances, shows that the mean frequency of the classes (1, 2) to (5, 6) in June is significantly higher than the mean frequency of the classes (0, 1) to (4, 5) in May ($t = 2.34$, 8 d.f., $P < 0.05$). When the mean frequencies of the classes (0, 1) to (3, 4) in April and (2, 3) to (5, 6) in June are compared, the increase turns out to be highly significant ($t = 4.95$, 6 d.f., $P < 0.01$). The most likely explanation for this phenomenon, which was also found by Shiff (1964c), is that young snails shelter as long as unfavourable conditions prevail and come out when conditions improve in June.

Fecundity

As for the growth curve, the fecundity curve used to calculate the f_x proportions by equation (13) was that for uncrowded laboratory populations (pooled results from the two cohorts). Since data were lacking after 11 months, the fecundity of older snails was taken in this calculation as equal to the mean fecundity during the last three weeks investigated.

The estimated maximum reproductive capacity in the field also follows a well marked annual cycle, the results from the two years being similar (Fig. 7): it reaches a maximum in May and a minimum in November. Thus, for the main cohort of snails (born in June), the conditions for reproduction are most unfavourable when these reach the age of highest potential fecundity, which is 5 months in the laboratory (Loreau & Baluku, 1987), i.e. in November. Furthermore, reproduction is strongly restrained throughout the year, since the maximum reproductive capacity was 5 to 62 times lower than the 593 eggs calculated from the data in the laboratory.

The variations in the maximum reproductive capacity profoundly modify the estimated fecundity curves of the successive monthly cohorts

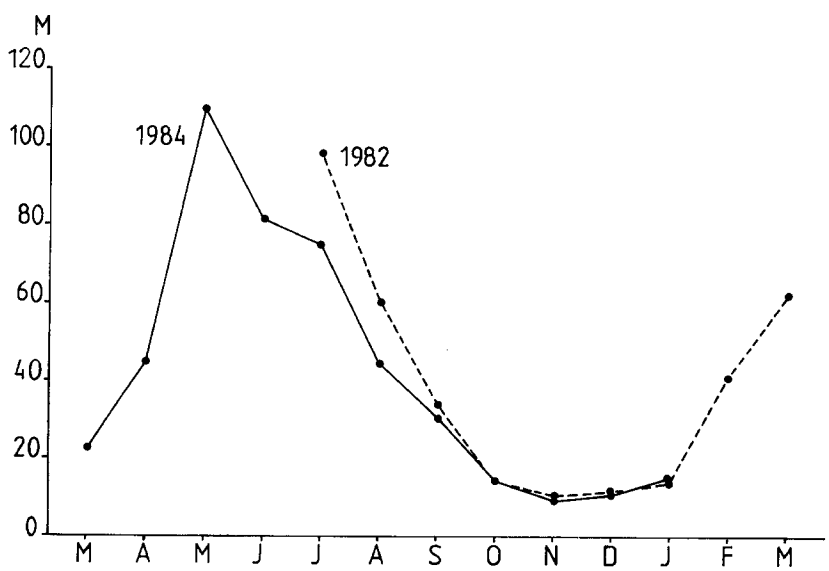


Fig. 7. Changes in the estimated maximum reproductive capacity in 1982 and 1984.

(Fig. 8), even though fecundity was calculated assuming a constant distribution of egg production among age classes. The snails born in December reach the highest fecundity—though still much lower than in the laboratory—because the time of their highest potential fecundity coincides with the time most favourable for reproduction. But snails born after April have a reduced breeding activity which tends to be delayed until the next year.

Demographic parameters

A short preliminary discussion is necessary before proceeding to the calculation of demographic parameters. Although it is mathematically possible to calculate demographic parameters such as the intrinsic rate of natural increase for successive cohorts, as O'Keeffe (1985a) did, this has no biological meaning because r, as well as its components b and d, represents the rate of increase (or, of birth or death) in time of a population reaching a stable age distribution under constant conditions, which is in very contradiction to the fact that we are interested in seasonal variations in r, i.e. we assume no constant conditions and no stable age distribution possible over the lifetime of the cohorts, in accordance with our previous results. This restriction does not apply to R_0, which is an average rate of reproduction per individual,

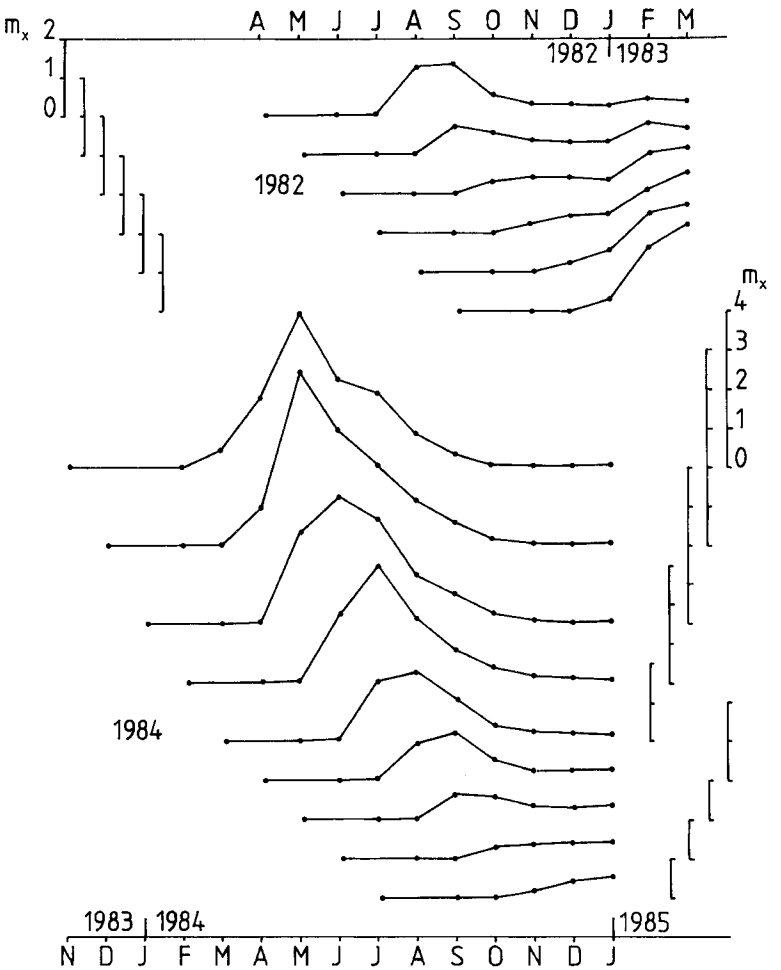


Fig. 8. Estimated fecundity curves of successive monthly cohorts in 1982 (above) and 1984 (below). The fecundity m_x is expressed in number of eggs per female per week for comparison with laboratory results.

and thus this was estimated for the cohorts that were followed over 6 months at least (Fig. 9).

However, our mathematical treatment allows biologically meaningful parameters r_t, b_t and d_t to be estimated, when the demographic variables are considered by month instead of by cohort. Fecundity estimates were obtained directly by month in equation (12), and equation (6) can be applied with transition probabilities calculated from month $t-1$ to month t for all age classes to get a survivorship curve characteristic of each month t instead of the survivorship curve of an actual cohort. Demographic parameters can then be estimated, which represent the intrinsic rate of increase, birth rate and death rate of a population that would reach a stable age distribution under the conditions prevailing at time t, i.e. suitable parameters to reflect the effects of environmental conditions on population dynamics (Fig. 10). In calculating the survivorship values, we observed the same rule as when survivorship curves for monthly cohorts were constructed, i.e. in each cohort replacing all class frequencies inferior to a frequency that follows by the latter. In addition, when there was a gap in the age structure of the population censused at a given month, the corresponding zero frequencies were replaced by one, in order to continue the survivorship curve until the last class encountered.

The figures for the net reproduction rate by cohort are very low (Fig. 9), two to four orders of magnitude lower than those found in the laboratory (Loreau & Baluku, 1987). This dramatic reduction is explained, not only by the combined reduction in both survivorship and fecundity, but also by a certain trade-off between them, the cohorts with the highest fecundity (born at the end of the year) suffering the most severe juvenile mortality, and the cohorts with the lowest mortality (born around March–April) reaching sexual maturity at a time of worsening conditions for reproduction. The result is that only the cohorts born at the beginning of the year (probably between January and April) can contribute on average to an increase of the population ($R_0 > 1$), while the main cohorts (born around June) contribute on average to a decrease of the population ($R_0 < 1$). The latter effect, however, is overestimated because the lack of continuous data over more than a year did not allow the breeding activity of the main cohorts in the next year to be taken into account.

The demographic parameters by month (Fig. 10) show a regular annual cycle in the instantaneous birth rate, but more erratic changes in the death rate. The resultant, r, also follows a yearly cycle with positive values only during a short period of the year, from April to June (but possibly from February onwards), which means that only during that period are conditions favourable to an increase of the population.

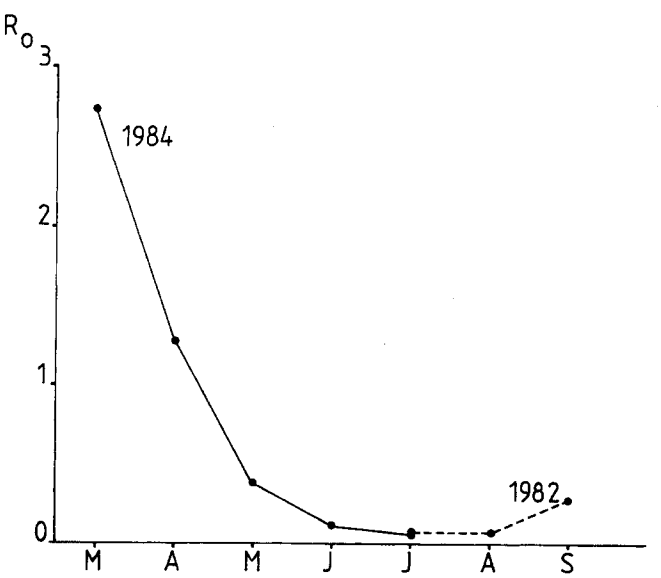


Fig. 9. Changes in the net reproduction rate of cohorts born in the months indicated, in 1982 and 1984.

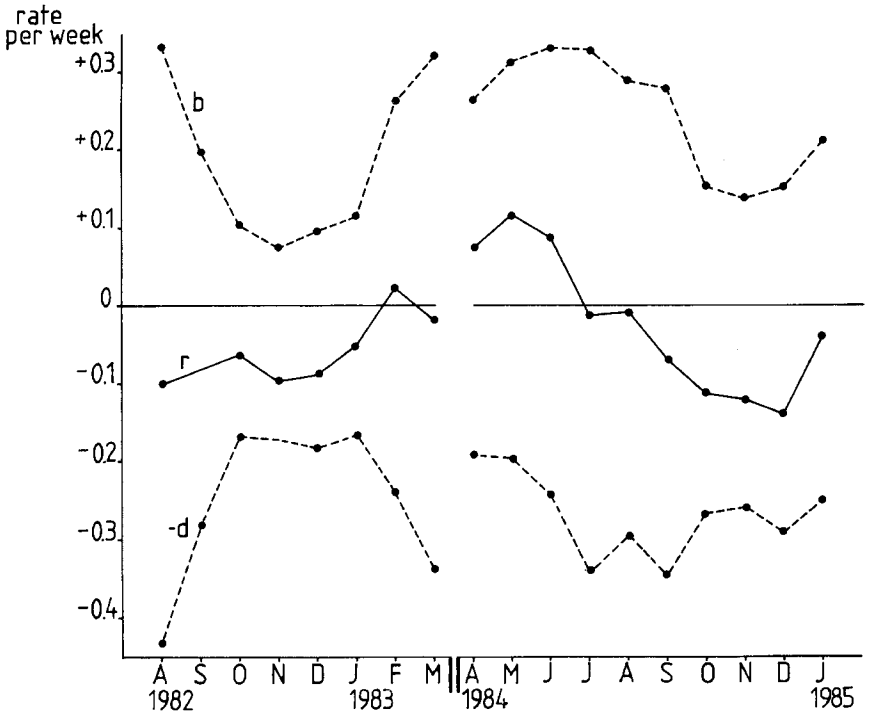


Fig. 10. Changes in the demographic parameters r, b and d characteristic of each month in 1982 and 1984. The results are expressed in rates per week for comparison with laboratory results.

Interestingly enough, r proves to be well correlated with the changes in egg density (compare with Fig. 1). The correlation between r_t and $\log(G_t/G_{t-1})$ is very highly significant ($r = 0.776$, 16 d.f., $P < 0.001$). Thus the single factor $\log(G_t/G_{t-1})$ is a good predictor of r_t.

DISCUSSION

Our demographic analyses show that the population dynamics of *Biomphalaria pfeifferi* in the field is quantitatively and qualitatively different from that in the laboratory. The main differences are: the discontinuity of the population dynamics, with one main generation per year, the very high juvenile mortality, the strongly reduced fecundity, and the marked seasonal variations in both factors.

The methods used in the analyses of course involve several approximations, which are likely to affect the results quantitatively, but their effects should be marginal compared to the amplitude of the above-mentioned phenomena and should generally have watered these down. It is not difficult to show that the assumption of no mortality during the egg stage in particular can only lead to an error of overestimation of survivorship values. Suppose instead a linear decrease in survivorship over the egg stage from $l_{-h} = 1$ (at laying) to l_0 (at hatching). Then, since the number of eggs collected at time t is equal to the egg production during the interval $(t - h, t)$ times the integral $\int_{-h}^{0} l_x dx$, and since l_0 was found to be close to 0, the integral $\int_{-h}^{0} l_x dx$ would be almost twice as low as in the case of no mortality. Accordingly the estimated egg production would be twice as high, which would reduce the transition probability P_0, and consequently all l_x estimates, by half. Thus the conclusion of a high juvenile mortality would be reinforced.

On the other hand, sampling must have acted to overestimate juvenile mortality, since both their small size, their lack of pigmentation, and their suggested sheltering behaviour under unfavourable conditions allow newly hatched snails to escape sampling. However, this only keeps the first weeks of the snails' life in the dark; the overall picture should not be altered.

During most of the unfavourable period, sheltering—probably in the sediments—is unlikely to prevent the death of the snails, which can hardly survive a long time in an environment like sediments, in which feeding and respiration are difficult, and in which they can easily be imprisoned because of the sedimentation process. A massive mortality in young snails was also noted by Eisenberg (1966) for another freshwater snail species in quite another biotope; it may be a general feature due to the greater sensitivity of juveniles to environmental conditions. Given its importance for the population dynamics in the field, the fate of the newly hatched snails would be worth investigating in more details.

The main environmental factors whose effects on *Biomphalaria pfeifferi* populations have so far been investigated are temperature (Sturrock, 1966; Shiff & Garnett, 1967; Appleton, 1977; de Kock & van Eeden, 1981) and hardness (Williams, 1970a, b; Harrison *et al.*, 1970). The importance of temperature was also emphasized in field studies on the population dynamics of other species (e.g. Shiff, 1964c; O'Keeffe, 1985a). Figure 11 summarizes the main environmental factors in the Virunga stream. Though they certainly determine the general level of the demographic variables and parameters, it is readily seen that neither temperature nor hardness can explain the observed features of the *Biomphalaria pfeifferi* population dynamics in the Virunga. The above-mentioned studies showed an optimum temperature between 25–29°C and an optimum calcium concentration around 12 mg/l for *Biomphalaria pfeifferi*. Thus in the Virunga temperature (between 17 and 22°C) is constantly under the optimum, and hardness (between 48 and 90 mg Ca^{++}/l approximately) constantly above the optimum. Yet the conditions for the increase of the population are best in May–June, when temperature is decreasing and hardness is increasing, and worst in November, when the reverse occurs. Also, even though temperature and hardness conditions are on average slightly less favourable than in the laboratory, this difference cannot account for the considerable reduction in survivorship and fecundity that occurs in the field.

Food limitation, which was pointed out in other species by Eisenberg (1966) and O'Keeffe (1985b), can be partly responsible for the seasonal changes in the population dynamics, in the form of a relative food shortage as was discussed in Loreau & Baluku (1987). *Biomphalaria pfeifferi* feeds on diatoms in the Virunga, and, from preliminary data on diatom density, it seems indeed that the increase of the population occurs in a period of increase in diatom density. However, food availability cannot explain the differences between field and laboratory results, since in the laboratory the snails were forced to eat plants which are abundant and yet disregarded in the field.

A major factor that distinguishes field from laboratory conditions is current. In the Virunga, current speed undergoes wide seasonal variations under the effect of rainfall, which is well known to be negatively correlated with *Biomphalaria pfeifferi* density (Webbe, 1965b; Parent, 1965). It usually increases considerably after the dry season, until November (the year 1984 was not typical in this respect), which coincides with the worst conditions for the increase of the *Biomphalaria pfeifferi* population. Current speed could be a crucial factor determining the population dynamics of snails, and would indeed explain many observed demographic features. The high juvenile mortality can be due to the inability of young snails to withstand brutal accelerations of the current after heavy rains. This factor is all the more likely since current speed was measured on fixed dates, and thus Fig. 11 does not include the strongest currents which follow heavy rains. Yet the current of 42 cm/s measured in November 1982 is enough to move mineral particles several millimeters in diameter (Nielsen, 1950). Therefore young snails, which have a much lower density, are bound to be carried away once removed from their support during floods. They probably shelter to escape strong currents, and are then exposed to the other mortality factors discussed above. The energy required to withstand the current could also bring about a reduced reproductive effort in adults, thereby explaining the low fecundity. In that context, the limitation of high-quality food such as diatoms could become important. What remains unexplained, however, is why the population starts decreasing during the dry season already. This cannot be attributed mainly to the further decrease in temperature and increase in hardness which occur during the dry season, because such changes should only reduce fecundity, but not survival (as it appears in the data of Sturrock, 1966; Shiff & Garnett, 1967; Harrison *et al.*, 1970; and de Kock & van Eeden, 1981). Detailed data on changes in food availability are necessary to know whether these could play a role during that period.

Lastly, it is worth pointing out the correlation that was found between the demographic par-

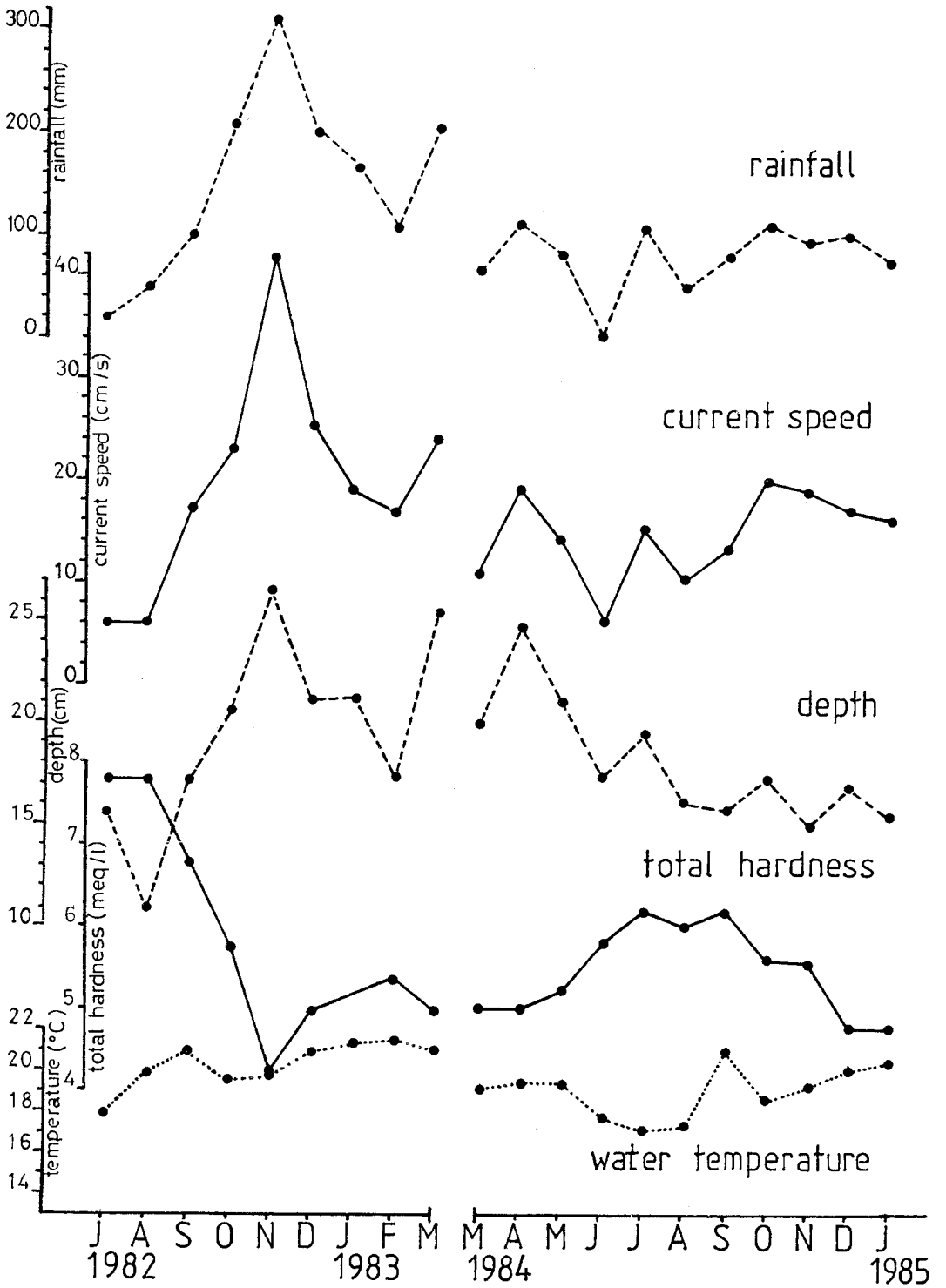


Fig. 11. Main environmental factors in the Virunga (biotope 4) during 1982 and 1984. Given the relatively constant proportions of Mg and Ca cations in the Virunga, a hardness of 1 meq/l is equivalent to about 11.5 mg Ca^{++}/l.

ameter r and the changes in egg density. The fact that r_t is well predicted by the single factor $\log(G_t/G_{t-1})$ may be of practical interest in biological control to detect the periods and conditions favourable to an increase of freshwater snail populations. We suggest that other studies should attempt to test the reliability of this correlation under different field conditions, and for different species.

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