A quest for the role of habitat quality in nature conservation
Klok, C.

Citation for published version (APA):

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: http://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
Assessing the effects of abiotic environmental stress on population growth in *Lumbricus rubellus* (Lumbricidae, Oligochaeta)

Abstract

A matrix model for the population dynamics of *Lumbricus rubellus* was formulated to assess the effects of abiotic environmental disturbances on the viability of the population. The population dynamic model is based on a description of individual growth, reproduction and mortality, which is partly derived from a simple model for the energy budget of an individual. The use of the energy budget model allows for establishment of causal relations between physiological influences of abiotic environmental stress and population performance.

Data on individual growth and reproduction (Ma 1983, 1984) are used to parameterise the model. The analysis shows that the length of the adult life span, and consequently the growth rate from birth to adulthood, is of overriding importance for the performance of the population.

Introduction

The dynamics of earthworm populations under different environmental conditions have been a major focus of interest in earthworm ecology over the last decades (S. Rundgren unpub. Ph.D. thesis University of Lund 1976; Edwards & Lofty 1977; Rozen 1988; Marinissen 1992). In population dynamic studies much attention has been paid to the influence of abiotic factors on the performance of earthworm populations. A major pattern arising from these studies is that soil humidity and soil temperature have dramatic effects on earthworm population densities (Lee 1985; Reinecke & Venter 1985; Reinecke et al. 1992). Unfortunately, relatively few studies have focused on the importance of processes at the individual level such as growth, reproduction and development. In particular, the dependence of population dynamics on food availability is poorly understood. However, interest in a more mechanistic and quantitative understanding of these processes on the level of a single individual is increasing (Daniel 1991).

Abiotic environmental stress factors potentially influence growth and reproduction of individual earthworms. The problem then, is how these influences subsequently induce changes at the population level, given that a population is dynamic and in tight interaction with other biotic factors, such as food resources and predators. Over the last decade a number of developments in mathematical population
dynamics and theoretical ecology have taken place that constitute a promising route to investigate such causal relations that span hierarchical levels of biological organisation (individual and population levels, respectively). These developments concern a broad class of models, usually termed ‘structured population models’ or ‘individual-based models’, that basically adopt the biological individual as the central unit in the modelling process. Using a description of the behaviour of a single individual (growth, development, reproduction and mortality) under a range of biotic and abiotic environmental conditions, these models employ bookkeeping-like operations to specify a model for an entire collection of individuals, i.e. a population. No further assumptions are made on the level of the population, the dynamics of which are therefore firmly based on the individual behaviour. Moreover, in these models individuals are allowed to differ from each other in age, size or other physiological traits. For a general introduction to these models see DeAngelis & Gross 1992.

In this paper a size-structured matrix population model was analysed to determine those aspects of individual life history with the largest influence on the matrix population growth rate of *Lumbricus rubellus*. In addition, the most likely reasons for population decline in the presence of environmental stress indicated by elevated copper concentrations were assessed.

Methods

Growth, development and reproduction of *Lumbricus rubellus* were modelled using a very simple model for the individual energy budget introduced by Kooijman and Metz (1984). The energy budget model allows us to link changes in energy allocation due to detoxification, to changes in the age-size relation of the individuals, and in turn, to population dynamical changes. The choice of the Kooijman and Metz energy budget model was inspired by practical reasons, since not enough information on individual growth, development and reproduction is available to unambiguously formulate a complete set of rules for the use of the energy assimilated by an individual. Parameter estimates for the energy budget model were derived from laboratory data on the growth, development and reproduction of *L. rubellus*, living under optimal conditions in sandy loam soil (Ma 1983, 1984). Individual survival was modelled phenomenologically on the basis of experimental data reported by Lakhani and Satchell (1970) for *L. terrestris* living in culture under optimal conditions.

The life cycle of an individual *L. rubellus* was subdivided into four distinct developmental stages: cocoon, juvenile, subadult, and adult. Data on individual growth and reproduction reported by Ma (1983) indicate that maturation is correlated with reaching a specific weight. Therefore, the developmental stages were assumed to correspond with particular size classes. The rate of progression through the different
developmental stages was derived from the energy budget model. Using a matrix model approach (Caswell 1989 and the short introduction below) all available information on the life cycle of *L. rubellus* was assembled to yield an estimate of the maximum population growth rate. The matrix approach was preferred because it allowed for estimation of the sensitivity of the maximum population growth rate to changes in the individual life history. In this way it is possible to associate the presence of an abiotic environmental stress factor with specific changes in individual life history, and therefore with changes in population growth rate.

As one type of abiotic stress, sublethal effects of copper were analysed. The model was used to derive an estimate for the critical threshold concentration for copper.

**A model for the individual behaviour of *L. rubellus***

In the energy budget model developed by Kooijman and Metz (1984) assimilated energy is allocated in a fixed proportion 1-\(K\) to growth and maintenance, and a proportion \(K\) to reproduction (Fig. 4.1). The central assumption in the Kooijman and Metz model is that growth and maintenance are competing more directly with each other for available energy than with reproduction. Energy requirements for maintenance always take precedence over growth and reproduction. Food intake is

![Figure 4.1](4.1)

Schematic representation of the energy channeling in the model of the individual behaviour of *L. rubellus* (after Kooijman & Metz 1984).
assumed to be proportional to surface area, and processes like growth and maintenance are proportional to wet weight. This leads to an attenuating growth curve under constant food conditions. The model further more assumes that individuals with different sizes have the same allometric relations, so that surface area is proportional to wet weight to the power of two thirds. Reproduction is assumed to start only after reaching a threshold size: the adult size. Individuals smaller than the adult size are assumed to spend the energy channelled to reproduction on the development of reproductive organs. For a complete derivation see Kooijman & Metz 1984.

These assumptions imply that under constant food conditions the individuals will grow according to the von Bertalanffy growth curve:

\[ l(a) = l_m - (l_m - l_b)e^{-\gamma a} \]  \hspace{1cm} (4.1)

where \( l_b \) equals the length of an individual at birth and \( l_m \) the maximum attainable length, \( \gamma \) the growth rate in weight per unit of time, and \( a \) age. Although reference is made to the quantity \( l \) as ‘length’, it should be kept in mind that \( l \) actually refers to wet weight to the power of one third. Because of the allometric relations \( l \) is only proportional to the real individual length. Given the von Bertalanffy growth curve, the assumptions that food intake is proportional to surface area \( l^2 \) and that a constant fraction \( 1-K \) of the assimilated energy is channelled into reproduction, imply that the reproduction rate of an individual of age \( a \) equals:

\[ m(a) = r_m[l_m - (l_m - l_b)e^{-\gamma a}]^2 \text{ for } l \geq l_{ad} \]  \hspace{1cm} (4.2)

where \( r_m \) equals the maximum reproduction rate per unit surface area, i.e. \( r_m l_m^2 \) equals the reproduction rate of an individual with maximum length, and \( l_{ad} \) the size of a maturing individual. The assumption that the onset of reproduction is triggered by reaching a threshold size is supported by experimental observation (Ma 1983).

Although Lumbricus rubellus is a well studied species, data on individual mortality of L. rubellus were virtually absent in literature. Therefore, mortality data of a species in the same genus, L. terrestris, were used to derive an estimated survival curve for L. rubellus. Lakhani and Satchell (1970) proposed the following survival curve for L. terrestris:

\[ S(t) = \left( \frac{1 - at}{1 + bt} \right)^k \]  \hspace{1cm} (4.3)

They estimated the parameter values in this equation, valid for L. terrestris to be \( a=0.0004 \), \( b=0.0056 \) and \( k=0.369 \). The parameter \( a \) has a clear interpretation as the inverse of the maximum life span of an individual L. terrestris.
To describe the survival of *L. rubellus* the same functional form as derived by Lakhani and Satchell (1970) was used and the parameters that involve the unit of time (both *a* and *b*) were scaled by the ratio of the maximum life span of *L. terrestris* and *L. rubellus*, respectively. The maximum life span of *L. rubellus* is set to 710 days (Ma, pers. comm.). Hence, *a*=0.0014, *b*=0.02 and *k*=0.369 were adopted as reasonable parameter values for *L. rubellus*. Figure 4.2 shows the resulting survival curve for *L. rubellus* adopted for the population model. Cocoons are assumed to develop in 42 days into juveniles (Ma, pers. comm.). The survival of the cocoons is determined by the percentage of viable cocoons which is set to 94% (Ma, pers. comm.).

**A matrix model for the population dynamics of *L. rubellus***

A matrix model was used to show how changes in individual behaviour of *Lumbricus rubellus* affect population growth rate. The structure of the matrix model is based on the life history of *L. rubellus*. The life cycle of an individual can be subdivided into four distinct developmental stages: cocoon, juvenile, subadult, and adult (Fig. 4.3). Given the number of individuals in each of these developmental stages in a population at some time *t*, the model determines the size and composition of the population one time step later at time *t* +1. As a basic unit of time one week was adopted. All individuals within each developmental stage are assumed to be identical and hence have the same probabilities to reproduce, to die or to move to the next stage. Within one
time step a single individual can (1) survive and stay in the same developmental stage with probability $P_1$, (2) survive and move to the next developmental stage with probability $G_i$ (provided it was not an adult), or (3) if in the adult stage, produce a certain number of viable cocoons, of which the average number produced per adult individual per unit time is indicated by the quantity $F_4$ (Fig. 4.3). The values of these transition probabilities are determined by the model for the individual behaviour, as defined in the previous section.

Let $c(t)$, $j(t)$, $s(t)$, and $a(t)$ be the number of cocoons, juveniles, subadults, and adults constituting the population at time $t$. On the basis of the life cycle graph the values of $c$, $j$, $s$, and $a$ one time step later can be derived by simple bookkeeping:

\begin{align}
\text{c(t+1)} &= P_1c(t) + F_4a(t) \\
\text{j(t+1)} &= P_2j(t) + G_1c(t) \\
\text{s(t+1)} &= P_3s(t) + G_2j(t) \\
\text{a(t+1)} &= P_4a(t) + G_3s(t)
\end{align}

These equations specify that the number of cocoons at time $t+1$ ($c(t+1)$) is equal to the number of cocoons at time $t$ that survived, but did not hatch during the time interval $t$ to $t+1$ ($P_1c(t)$), plus the number of viable cocoons produced by the adults present at time $t$ during the time interval $t$ to $t+1$ ($F_4a(t)$).

The number of juveniles at time $t+1$ ($j(t+1)$) is equal to the number of
juveniles at time \( t \) that survived and stayed in the juvenile class during the time interval \( t \) to \( t+1 \) (\( P_2 j(t) \)), plus the number of cocoons that developed into juveniles during the time interval \( t \) to \( t+1 \) (\( G_1 c(t) \)).

The equations for \( s(t+1) \) and \( a(t+1) \) can be interpreted analogously. Let \( n(t) \) be a vector denoting the number of individuals in the different developmental stages at time \( t \) (‘the population vector’):

\[
n(t) = \begin{pmatrix} c(t) \\ j(t) \\ s(t) \\ a(t) \end{pmatrix}
\]

Using the population vector, \( n(t) \), the equations shown above can be reformulated, in matrix notation as:

\[
n(t+1) = Mn(t)
\]  

with

\[
M = \begin{pmatrix} P_1 & 0 & 0 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}
\]

The matrix \( M \) is usually referred to as the population projection matrix and can be interpreted as a mathematical representation of the life cycle graph.

Caswell (1989) provides an extensive introduction to the theory of matrix models, including their formulation, analysis and application. Here only some basic properties of matrix models are briefly sketched.

The long-term behaviour of \( n(t) \) depends on the eigenvalues of the population projection matrix. If the environment remains constant, the population will finally grow with a rate equal to the largest eigenvalue of \( M \). The largest eigenvalue of \( M \) is directly related to the maximum population growth rate: \( \lambda_m = e^r \), where \( r \) equals the maximum population growth rate, and \( \lambda_m \) the largest eigenvalue. The sensitivity of this largest eigenvalue with respect to changes in the life cycle parameters can be calculated. For example, it is possible to determine the relative contribution of the entries of the matrix \( M \) to the largest eigenvalue. If stress factors that influence the individual behaviour are considered and hence the entries of \( M \), a sensitivity analysis can be used to determine that specific developmental stage or process, which would cause the largest change in the maximum population growth rate. In other words, it is possible to determine which developmental stage or process is most vulnerable to abiotic
environmental stress when judged from the perspective of the population.

As mentioned before, the size-age relations were used for individual growth and reproduction and the age relation for survival described in the previous section to derive expressions for the life cycle parameters \( P, G, \) and \( F. \)

For a detailed derivation of these relations between the model of the individual behaviour and the life cycle parameters of \( L. \ rubellus, \) reference is made to Klok & De Roos 1996.

**Model parameterisation**

Experimental data from Ma (1983, 1984) were used to parameterise the energy budget model. Figure 4.4 shows that the growth rate and maximum size of an individual \( L. \ rubellus \) decreases in the presence of increased copper concentrations. The figure indicates that individuals reach the subadult and adult stages at identical weights of 500 mg and 780 mg, respectively. These weight thresholds are equivalent with a length at reaching subadulthood and adulthood of \( l_s=7.9\text{mg}^{1/3} \) and \( l_{ad}=9.2\text{mg}^{1/3}, \) respectively. These threshold values do not change when the individual experiences an increased copper concentration in its environment.

![Figure 4.4](image-url)

**Figure 4.4**

Effect of copper on the growth and development of \( L. \ rubellus \) in sandy loam soil (after Ma 1983). Open arrows indicate the mean age and size at which individuals entered the subadult stage (defined as individuals that show the first signs of a clitellum), filled arrows indicate the mean age and size at which individuals become adult (that is, reproductively active).

-● control, ○ Cu 60 mg kg\(^{-1}\), ▼ Cu 145 mg kg\(^{-1}\), and ▽ Cu 362 mg kg\(^{-1}\).
Table 4.1
The estimated values of the life cycle parameters in the population projection matrix, based on data from Ma 1983, 1984 and Lakhani & Satchell 1970, and their relative contribution (in %, in brackets) to the population growth rate.

<table>
<thead>
<tr>
<th>Life cycle parameters</th>
<th>Cocoon</th>
<th>Juvenile</th>
<th>Subadult</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_i$</td>
<td>0.83 (16.4)</td>
<td>0.87 (21.4)</td>
<td>0.70 (9.1)</td>
<td>0.97 (36)</td>
</tr>
<tr>
<td>$G_i$</td>
<td>0.16 (4.3)</td>
<td>0.10 (4.3)</td>
<td>0.27 (4.3)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>$F_i$</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0.99 (4.3)</td>
</tr>
</tbody>
</table>

Since data on individual survival of *L. rubellus* could not be found, increased copper concentrations were assumed only to cause sublethal effects and individual survival is hence always optimal. The estimated values of the life cycle parameters are given in Table 4.1.

Results and discussion

The population projection matrix $M$, parameterised for a *Lumbricus rubellus* population living under unstressed conditions, was used to calculate the maximum population growth rate, which equals 0.012 day$^{-1}$. Obviously the absolute value of the maximum population growth rate depends heavily on the precise experimental data that were used for the parameterisation. Comparisons between the population growth rates for unstressed and stressed situations are, however, more robust. Following the procedures of Caswell (1989), the sensitivity of the maximum population growth rate (calculated from the control population) was determined to changes in the life cycle parameters.

The results of the sensitivity analysis can be summarised by the relative contribution of every single entry in the matrix $M$ to the realised maximum population growth rate (Table 4.1). The results indicate that the probability of survival as an adult contributes most to the population growth rate (36%). Consequently, the maximum population growth rate will be most sensitive to changes in this parameter ($P_A$), ($P_2$), the probability to survive and remain in the juvenile stages is the next most important factor. Changes in the reproductive output ($F$) and the probability to survive and grow to the next stage ($G$) are of less importance to the population growth rate.

The life cycle parameters ($P$) and ($G$) are functions of both survival and growth through the stages. This makes a precise interpretation of the outcome of the sensitivity
Figure 4.5
Effect of copper on the calculated population growth rate per day.

analysis on \((P)\) and \((G)\) difficult. To overcome this problem a more detailed sensitivity analysis on the underlying parameters, survival probability and growth probability, was carried out. The results of this analysis, which are not reported in detail, again indicate that the survival probability during the adult period is of major importance to the population growth rate.

Due to the fact that the size which an individual has to reach to become reproductive is set to a specific value, and the individuals have a fixed life span, the value of the entry \((P_4)\) in the matrix is primarily determined by the duration of the adult period. This means that if an individual reaches the adult stage at a late age the value of \((P_4)\) will be low, as will the maximum population growth rate.

In this study data on reduction in individual growth due to copper stress (Ma 1983) were analysed. The formalism of the energy budget model was used to interpret the reduction in individual growth as being due to increased maintenance requirements for detoxification. Basically, the changes in the individual growth curve due to copper stress (Fig. 4.4) lead to different estimates of the parameters \(l_m\), \(\gamma\) and \(r_m\) in the growth
and reproduction functions. These changes in the energy budget parameters lead to changes in the life cycle parameters which result in a changed population growth rate. The parameters $l_m$, $\gamma$ and $r_m$ are actually composite parameters, made up by quantities that refer to characteristics of the underlying energetic processes. The composite nature of the energy budget parameters leads to interrelation between them which has to be taken into account during the parameter estimation. For details on the energy budget parameter estimation see Klok & De Roos 1996.

Figure 4.5 shows the effect of increased copper concentrations on the population growth rate. Extrapolating the decline in the population growth rate of lower concentrations of copper (65 and 145 mg, respectively) a population growth rate equal to zero is attained at a concentration of around 300 mg Cu kg$^{-1}$ sandy loam soil. This implies that in the experiments of Ma (1983, 1984) the population treated with 362 mg copper will die out. The extinction is the result of the severe reduction in individual growth under these conditions. The maximum attainable length $l_m$ at such high copper concentrations is smaller than the maturation length $l_{ad}$. Hence individuals never mature and are incapable of reproduction.

The Critical Threshold Concentration (CTC) for copper as estimated from the model (300 mg kg$^{-1}$ soil) is a conservative estimate, because only the effects on individual growth due to copper are taken into account. The estimate holds for earthworms living under otherwise optimal conditions, i.e. food is abundant and mortality is low (predation is not a factor). *L. rubellus* living under field conditions will probably face a combination of additional stress factors. Therefore it is expected that the estimation of the CTC for copper will be an overestimate. Field studies done by Ma (1988) show a steep decline in the size of field populations when copper concentrations rise to 200 mg kg$^{-1}$. Comparing the results of Ma (1988) it is concluded that the model gives a prediction of the CTC for copper that is in reasonable agreement with the empirical data.

The energy budget model provides a way to assess how effects on the individual level translate into population level consequences. One can circumvent the necessity of translation by doing experiments at the population level itself. However, this is a costly approach which presents problems in the interpretation of effects. Besides there is a substantial risk of not detecting effects because of the erratic behaviour of populations. Moreover, experiments with toxicants on populations in their natural environment might not be ethically justifiable. Parameterisation is one of the bottlenecks in population dynamic model studies. It is hard to find consistent data sets in literature.

The results of the model study indicate that the major danger for *L. rubellus* populations under abiotic environmental stress is that individuals fail to reach the adult size within their life span. If the stress on individual behaviour in growth and reproduction is not extreme, i.e. when the individuals do reach the adult size, then the length of the lifetime spent as an adult individual is of most importance to the
population growth rate. This primarily implies that individuals have to grow quickly through the preadult stages. The rate of reproduction when judged from the perspective of the population is of much less importance. Future studies, aimed to increase the understanding of the impact of environmental stress on the population dynamics of *L. rubellus*, should take into account the implications of the stress factors for growth and development during the preadult stages.

**References**


Ma, W.C. 1984. Sublethal toxic effects of copper on growth, reproduction and litter breakdown activity in the earthworm Lumbricus rubellus, with observations on the influence of temperature and soil pH. Environmental Pollution (Series A) 33: 207-219.


