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Using process-based modelling to analyse earthworm life cycles

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Abstract

To understand the life cycle of an organism, it is important to understand the physiological processes that govern growth and reproduction. In this paper, we re-analyse a life-cycle data set for the earthworm *Eisenia veneta*, using a process-based model. The data set comprises measurements of body size and cocoon production over 200 days, at two temperatures (15–25 °C) and two densities (five and 10 worms per container, but with the same worm:soil weight ratio). The model consists of a set of simple equations, derived from Dynamic Energy Budget (DEB) theory. The dynamics of growth and reproduction are simultaneously described by the model, using very few parameters (five parameters for four curves). This supports the use of this model for efficient analysis of earthworm life-cycle data, and to interpret the effects of stressors. However, there was considerable inter-individual variation in the response, hampering the interpretation of the temperature and density effects. A temperature increase corresponded to an increase in the rate constants for growth and reproduction (with the same factor), without affecting the other parameters, as expected from DEB theory. Changing the earthworm density hardly affected the growth curves, but had an unexpected effect on reproduction: at higher densities, the worms start to produce cocoons at a larger body size and the maximum reproduction rate was lower. This study confirms the use of DEB as a reference model for earthworms, and using this model, we can recognise that temperature has a predictable effect on the life cycle of *E. veneta*. Furthermore, this analysis reveals that the effects of density are less clear and may involve a change in energy allocation that requires further study.

Keywords: Earthworm; *Eisenia veneta*; Life cycle; Growth; Reproduction; Temperature; Density

1. Introduction

To understand the life cycle of an organism, it is important to understand the physiological processes that govern growth and reproduction. However, life-cycle studies are usually more descriptive than mechanistic. The various endpoints (e.g. growth and reproduction) are often treated as isolated processes, whereas they are in fact closely interrelated. For example, reproduction generally starts at a certain minimum body size, which means that any treatment that slows growth automatically leads to a delay in reproduction (e.g. Klok and De Roos, 1996, for copper in *Lumbricus rubellus*, Jager, 2005, for food density and temperature in nematodes). Furthermore, body size determines reproduction rates, because the organism converts food into offspring, and feeding rates relate to body size. To increase our understanding of life histories, the different aspects should be integrated into a single model framework. We here use the theory of Dynamic Energy Budgets (DEB, Kooijman, 2000; 2001; Nisbet et al., 2000) to investigate these relationships. This theory describes how individuals acquire and utilize energy, based on a set of simple rules for metabolic organization, treating the organism as a system with a closed mass and energy balance.

The advantage of such a model-based approach is that it facilitates the interpretation of observed effects of stressors on the life cycle, and allows for the prediction of effects under other circumstances (e.g. for the combined effects of toxicants and food limitation, Jager et al., 2004). To illustrate the usefulness of this process-based model, we analyse data from life-cycle experiments with the earthworm *Eisenia veneta* (formerly called *Dendrobaena veneta*), using a set of simplified equations based on DEB theory. This data set was published earlier by Viljoen et al. (1992). *E. veneta*, a species from the northern hemisphere, is not a typical soil-dwelling species, but is usually confined to

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accumulations of organic debris (decaying leaves, manure heaps). For this reason, this species has been identified as a potential candidate for vermiculture (the transformation of organic waste to compost using earthworms) (Edwards and Bater, 1992; Lofs-Holmin, 1986). Furthermore, this species is very popular among anglers, and many breeders specialize in this species. Clearly, a thorough mechanistic understanding of the life-history aspects of this species can have both scientific as well as economic benefits.

2. Methods

2.1. Experimental

Details of the experimental set-up have been described by Viljoen et al. (1992). Day-old hatchlings of *Eisenia veneta* (average weight 23 mg, SD 5.2) were placed into a cattle manure substrate with a moisture content of 75–80%. The worms were maintained under constant temperatures (at 15 or 25 °C), and in two densities (five or 10 individuals per container). The densities only differed with respect to the number of worms per container; in the high density, more substrate was used to keep the number of worms per mass of substrate constant (the data for 10 worms/container were not used in the original analysis by Viljoen et al.). Fifty grams of the cattle manure substrate was provided per worm, which ensured sufficient food per worm for the experimental duration (ad libitum conditions). Additional feeding took place after 20 days, and every 10 days thereafter, by adding equal amounts of manure per worm to the containers. At each temperature, there were five containers with five worms, and two with ten. Every five days, the worms were weighed, and the number of mature worms (judged from the presence of a clitellum) and cocoons were reported.

2.2. Models

A consequence of the DEB theory is that organisms should grow according to a Von Bertalanffy growth curve, as long as the food density is ad libitum, or remains constant. The rationale, underlying this specific curve, is that food uptake is generally proportional to a surface area (squared length for isomorphs), whereas maintenance costs are proportional to volume (cubed length) (Kooijman, 2000). When the organism grows, volume increases more rapidly than surface area, and at a certain body size, all of the resources allocated to growth and somatic maintenance are used for the latter, and growth ceases. This conceptual view of growth also explains why growth rates and ultimate body size decrease at lower feeding rates.

To simplify the equations, we will use scaled lengths, i.e. body length as fraction of the ultimate length at abundant food (L_m). Scaled lengths are denoted by a lowercase symbol (l), absolute length by uppercase (L). As long as the organism does not change its shape, in practice, any length measure can be used (e.g. total body length, body width, or length of a specific organ). In this case, body size for *E. veneta* were determined as wet weight. These weights can be translated to a length measure by a recalculation to body volume (assuming a constant specific density of 1 g cm^{-3}), and taking the cubic root of the volume. The length measure thus obtained is called a ‘volumetric body length’.

At constant food levels, the DEB theory reduces to the Von Bertalanffy growth equation, giving scaled length as a function of time (Kooijman and Bedaux, 1996)

$$\frac{d}{dt}l = r_B(f - l) \qquad (1)$$

where f is the scaled ingestion rate (as fraction of the maximum rate), and r_B is a growth rate constant (dimension per time). When f and r_B are constant, Eq. (1) can be integrated

$$l = f(1 - e^{-r_B t}) + l_0 e^{-r_B t} \qquad (2)$$

where l_0 is the initial scaled length. The growth rate (r_B) has, within DEB theory, a special relationship with maintenance costs and thus with the ultimate size (see Kooijman and Bedaux, 1996). This equation produces a sigmoid curve of body weight or volume, but a non-sigmoid curve for body length (i.e. a curve with strictly decreasing slope, see Fig. 1). Changing the food level changes the relative ingestion rate (f) in Eq. (1) and (2). Less food (or food of lower quality) leads to a smaller ultimate size, as was shown for *E. fetida* by Neuhauser et al. (1980), and for *E. veneta* by Fayolle et al. (1997).

DEB theory specifies that the reproduction rate (R in offspring per time) is a function of the body size (or scaled length l), as given by Kooijman and Bedaux (1996)

$$R(l) = \frac{R_m}{1 - l_p^3}\left(\frac{g + l}{g + f} f l^2 - l_p^3\right) \qquad (3)$$

where R_m is the maximum reproduction rate, and l_p the scaled length at the start of reproduction. This equation is a simplification of the full DEB theory, specifically intended for the analysis of toxicity data. The close relationship between body size and reproduction was also shown for *E. fetida* in direct experiments with varying food levels (Reinecke and Viljoen, 1990a). The energy investment ratio (g) is a dimensionless parameter, with the interpretation of the cost of new biomass relative to the total available energy for growth and maintenance. For water fleas, g is probably close to 1 (Kooijman and Bedaux, 1996). However, the model is not particularly sensitive to this parameter, unless different food levels are compared. To facilitate the comparison of the model to reproduction data, Eq. (3) is integrated and compared to the cumulative number of cocoons produced per mature worm.

Temperature has, within DEB context, a predictable effect on the organism. A temperature increase is expected to