The application of DEB modeling as a management tool for the species Arenicola marina and A. defodiens

Lola DE CUBBER

PhD student Laboratoire d'Océanologie et de Géosciences UMR 8187 LOG 62 930 Wimereux, France Université Lille 1

Thank you for these five weeks of interesting course!

Introduction

Arenicola spp. (Annelid polychaeta), are marine benthic coastal ecosystem engineers playing a key role both in bioturbation of soft sediments and in the local trophic network. In many coastal areas and particularly in the Region 'Hauts de France' (North of France, English Channel), lugworm's specimens are intensively dug by professional and recreational fishermen which might affect their stocks. Within a local MPA, the 'Parc naturel marin des estuaires picards et de la mer d'Opale', two species are commonly found: *Arenicola marina* and *A. defodiens*, but the scarcity of knowledge concerning their biology, ecology, and their populations' dynamics make their management a headache.

Dynamic Energy Budget (DEB) theory is a formal theory for the uptake and use of substrates (food, nutrients and light) by organisms and their use for maintenance, growth, maturation and propagation (Kooijman, 2010).

The aim of my PhD is therefore to bring more knowledge on these species' biology and ecology (mainly their lifecycle) to assess their potential growth and reproduction among the MPA thanks to DEB modeling.



Figure 1 : Arenicola marina's lifecycle according Farke and Berghuis (1979) and Hardege et al. (1998). Pictures are taken from Farke and Berghuis (1979). Adapted by Lola De Cubber.

The biology and ecology of Arenicola marina and A. defodiens

Both species have a bentho-pelagic life cycle: adults and juveniles live within the sediment in a U-shaped gallery, feeding of the organic matter it contains, whereas larval and post-larval stages are pelagic and spread using currents among the water column. Little is known about the life-cycle of *A. defodiens*, but the one of *A. marina* has already been described by various authors and is represented in Figure 1.

The application of DEB modeling

An energy budget is the specification of the uptake of energy from the environment by an organism (feeding and digestion) and of the use of this energy for various purposes: maintenance, development, growth and reproduction. A dynamic energy budget follows the changes of these fluxes during the life cycle of an organism. The energy fluxes of a standard energy budget for a juvenile or adult are represented on Figure 2.



The Figure 2 can be translated mathematically as follows:



Figure 3: Schematic representation of the DEB model and the associated equations. Parameters and fluxes are detailed in table 1 and 2.

The aim of the DEB theory is to predict the growth and reproduction of individuals according to the expression of the different energy compartments presented on Figure 3.

Indeed, we can determinate:

- The physical length L_w from the structural volume V: L_w = $V^{1/3}/\delta$ (δ being the shape coefficient of the species)
- The dry weight W_d, being the weight of structure + the weight of reserve and the reproduction buffer: W_d = d_d.V + $\frac{w_E}{\mu_E}$ (E+E_R) (d_d being the density of dry structure, μ_E the specific potential of reserve and w_E the molar weight of reserve)

All the notations are taken from notation part of the course's book.

The values for the three compartments needed (reserve, reproduction buffer and structure) are then obtained from the expressions of fluxes (table) adjusted for the temperature encountered in the environment thanks to the Arrhenius temperature T_A according to the expression $\dot{k}(T) = \dot{k_1} \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)$ considering the individual only encounters favorable temperatures.

Flux	Expression	
Ingestion	$\dot{p}_X = \{p_{Xm}^{\cdot}\}fV^{2/3}$	
Assimilation	$\dot{p}_A = \kappa_X \dot{p}_X$	
Mobilization	$\dot{p}_C = E \frac{\dot{v}V^{2/3}[E_G] + \dot{p}_S}{\kappa E + V[E_G]}$	
Somatic maintenance costs	$\dot{p}_S = [\dot{p}_M]V + \{\dot{p}_T\}V^{2/3}$ (there might be costs for osmoregulation to different salinities for lugworms if any $\{\dot{p}_T\}=0$)	
Maturity maintenance costs	$\dot{p}_J = \dot{k}_J E_H$	
Growth	$\dot{p}_G = \kappa \dot{p}_C - \dot{p}_S$	
Reproduction	$\dot{p}_R = (1 - \kappa)\dot{p}_C - \dot{p}_J$	

Table 1: The different fluxes and their mathematical expression

The consequences of other phenomena like starvation can also be added to this basic model, and depend on the considered species. But before complicating the model, we first need to estimate the parameters of the basic model.

The estimation of DEB parameters

The 12 primary parameters needed for the implementation of the basic DEB model are presented in Table 2. Compound parameters can also be used to estimate the primary parameters.

There are different ways to estimate DEB parameters and they are usually combined to get the best set of possible parameters. First, sampling and experiments can be done to assess part of the parameters (see Van Der Meer et al. 2006 for example). From a first set of parameters, the package DEBtool and its functions also enable the calculation of most of the primary parameters (see Kooijman et al. 2008). Finally, the covariation method enables to estimate the parameters of a species from a combination of the known parameters of this species (zero variate data), and experiments with length or weight over time and measures of fluxes (univariate data) (Lika et al., 2011).

In our case, since *A. marina* and *A. defodiens* are really close from both an ecological and a taxonomic point of view, the zoom factor (Kooijman et al. 2008) could help in the estimation of some of the DEB parameters.

Description	Symbol	Dimension
Surface-area specific searching rate	$\{p_{Xm}^{\cdot}\}$	eL ⁻² t ⁻¹
Surface-area specific maximum assimilation rate	$\{p_{Am}^{\cdot}\}$	eL ⁻² t ⁻¹
Fraction of food energy fixed in reserve	κ _X	-
volume-specific costs of structure	$[E_G]$	eL ⁻³
Energy conductance	\dot{v}	Lt ⁻¹
Surface-area-specific somatic maintenance	$\{\dot{p}_T\}$	eL ⁻² t ⁻¹
Volume-specific somatic maintenance	$[\dot{p}_M]$	eL ⁻³ t ⁻¹
Specific maturity maintenance rate	, kj	t ⁻¹
Allocation fraction	к	-
Reproduction efficiency	κ_R	-
Maturity at birth	$E_{H^{b}}$	е
Maturity at puberty	E_{H^p}	е

Table 2: The 12 primary parameters of the DEB theory

In Kooijman et al. (2008) y_{VE} et y_{EX} replace the parameters κ_X and $[E_G]$ but in the model expressed in energy, these last two are more usefull.

Linking DEB to the life cycle of lugworms

During its lifecycle, an individual will not experience all the time the same fluxes depending on if it feeds or not, or if it reproduces or not. In DEB theory, only three stages are considered, and the DEB vocabulary might differ slightly from the biological one, they are: the embryo, which is the stage that does not feed after fertilization, the juvenile stage, when feeding happens but nor reproduction, and the adult stage when both feeding and reproduction happen.

In lugworms, larvae are not able to feed until metamorphosis (see figure) that is to say that until $E_H = E_H^b$ (birth is the moment when the individual starts to feed in DEB theory), there is no feeding flux or assimilation flux and $\frac{dE}{dt} = -\dot{p}_C$. Moreover, they do not have enough complexity yet to be able to produce gametes and the reproduction flux goes to maturity (which represents in this case the complexification of the individual).

In lugworms, the second DEB - stage is the juvenile one that happens after metamorphosis, when the individual already developed a digestive tract and is now able of feeding. Feeding and assimilation are not null anymore, but individuals are not able yet to produce gametes. A change of shape also happens between the larval stage and the juvenile stage. For *A. marina*, there are two juvenile stages (see Figure 1). The first juvenile stage, also called "post-larva" feeds on the suspended particles in the water column. After a certain period of time, they migrate to the adult grounds and start feeding on the organic matter present at the sub surface of the sediment: this is the second juvenile stage. At this time, the juvenile stage(s) of *A. defodiens* has(have) not been described yet. Since the habitat changes from the pelagic environment where variations are quite smooth for the larval and juvenile 1 stages (post-larva) to the benthic environment were environmental variations are drastic for the juvenile 2 and the adult phase, a change in the Arrhenius temperature might also be noted between these stages.

Finally, the adults keep the same nutrition mode as the juveniles (second stage) but acquire the ability to reproduce (which is when $E_H > E_H^p$) and the energy flow formerly allocated to maturity is now allocated to a reproduction buffer that empties, in the case of lugworms, once a year in autumn, when oocytes and spermatozoids are expulsed.

The parameter estimation for these species

The ability to make the difference between *A. marina* and *A. defodiens* happened in 1993 (Cadman and Nelson-Smith 1993), thus, most of the life history traits of these species and the parameters recorded in the literature before that date (which represents most of it) must be considered with caution and verified whenever possible.

Life-history traits have been recorded since 2015 for both species. The next steps are then according to Kooijman et al. (2008) to be aware of the growth and reproduction of a individual at a single food density and at different food densities.

I am now recording the growth (length and weight) of juveniles of *A. marina* and *A. defodiens* under two different food conditions (starved and well fed) at a single temperature (15 °C). This should give us \dot{r}_B at $f \simeq 1$ which would enable us to know g, \dot{k}_M , \dot{v} , U_{ϵ}^0 , U_{ϵ}^b .

The next step will be to record the reproduction of these species and verify its timing (duration of the larval stage and age at metamorphosis, ...) in autumn, when the spawning period happens.

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