Dynamic Energy Budget theory

An explosive first meeting;

The past six months were probably the most exciting months of my student days. First of all I started my first internship at the Dutch Royal Institute for Sea Research (NIOZ) at the island of Texel. From the moment I started my research, about the foraging behaviour of the shore crab *Carcinus maenas*, I gained a lot of practical experience. My supervisor, Jaap vd Meer, made a great contribution to this by letting me free in setting up my experiments and solving my own problems.

How surprising, it was Jaap who introduced me to the DEB-theory. To what? Yes, that is what I said the first time I heard the word DEB. Oh, the Dynamic Energy Budget theory. I had never heard of that theory and I was really surprised by that. In fact, nobody I know has ever heard of that theory. But Jaap was enthusiastic enough to start telling about the theory. He started in the most simple way, by telling the big messages. Metabolism is organized in the same way within all animals. Everybody has at least one structure and one reserve. Energy is supplied by the intake of food, this food is assimilated and goes to a reserve pool. The amount of assimilated food is proportional to $V^{2/3}$. The reserve pool is not mend to be a storage place. No, one fraction called kappa (κ) goes to the volume as maintenance and growth. Again, κ is proportional to the volume. The other fraction, 1-κ, goes to maturity and reproduction (after completion of maturity). Well so far so good. But then Jaap proposed to follow the DEB course. To be exact, this was on a Tuesday, while the course would start on Thursday. So, head over heels, I signed in for the course and hid my head into the DEB-book.

Already at the first meeting in Amsterdam I knew it. This would be a hardcore course for me. You cannot try to understand the DEB-theory all at once. Especially not when you have never heard of the theory before. The formulas written in the book make it very complicated to follow the major messages , the one which are really important. I think your latest version "a summary of concepts" is very good. It contains no formulas at all and that really helps to understand the theory better. I haven't read it yet though, but I will because it also looks more attractive to read. I think it is a good idea to introduce people who have never heard of DEB (and are no theoretical biologists), first to this summary of concepts.

It is certainly not possible to understand this theory at once. I noticed that it is far more effective when you follow the course several times. Every time you read the same piece of text, you learn something more about the DEB-theory. Messages you miss the first time, you pick out the second time. Also the discussions with other peoples on blackboard and during the symposium, help to understand the theory more and more. Besides, you understand parts which another one doesn't while it is also the other way around.

The biggest issue I run into, was the use of Octave and DEBtool. The use of these programs is very difficult, if not impossible if you see it for the first time. Maybe it is a good idea to give some kind of mini-course about the use of these programs on forehand. Or recommend an existing course, if there already is one, for the use of Octave/Matlab. Now I have the feeling I missed all the fun because I barely succeeded in running files in Octave. Besides, this makes it very difficult to give a good contribution to the add-my-pet assignment. In my feeling, I really performed under my capacities on this part of the course.

Nevertheless, it is a fact that the DEB-theory is an interesting theory. The course and excitement of you, Bas, really provoked my interest. Thanks to that, I certainly plan to lose myself a second time in the theory. But not before the first explosive meeting has sunk a bit.

Data *Sepia officinalis*

The literature can give you a lot of information about the sepia. The most important information I summarized in a table:

Parameter	Waarde	Reference
Age at birth (Ab)	45 d	Domingues et al 2008
Age at puberty (Ap)	70 d	lost
Length at birth real data	6-10 mm	Domingues et al 2008
Length at puberty real data	45 mm	lost
Length at maturity real data	140 mm	Laptikhovsky et al. 2003
Max. length literature	300 mm males/250 mm females	Nesis 1987
Max. length caugth	400 mm	non trustive site
Wet weight at birth	0,15 gram	Domingues et al 2008
Wet weight mature	2800 gram	non trustive site
Lifespan	8 months-2 years	Laptikhovsky et al. 2003
Max. lifespan	2 years	Laptikhovsky et al. 2003
Egg length when ripe	6,45-7,53 mm	Laptikhovsky et al. 2003
Egg weigth when ripe	109,9-167,5 mg	Laptikhovsky et al. 2003
Potential fecundity	1000-3000 eggs	Laptikhovsky et al. 2003
actual spawning	500-1500 eggs	Laptikhovsky et al. 2003
Max. feeding rate sepia 44.4 gr	3,46 g/day = 63,73 kJ/day	Domingues et al 2008
Conversion rate hatchlings	35-50 %	Nixon & Mangold 1998
Conversion rate juveniles	19%	Domingues et al 2008
Assimilation efficiency juveniles	89%	Domingues et al 2008
Uptake juveniles	1,61 kJ per g/day	Domingues et al 2008
Absorbtion juveniles	1,43 kJ per g/day	Domingues et al 2008
Produced energy juveniles	0,25 kJ per g/day	Domingues et al 2008
Maintenance costs newly hatched	2,76 % DW and 3,26 % WW	Grigoriou & Richardson 2008
Maintenance costs > 2gram	1,86 % DW and 2,21 % WW	Grigoriou & Richardson 2008

Most of these data are obtained by a temperature of 20 °C. Accept those of Laptikhovsky et al. (2003). These data were obtained from sepia caught in the Aegean sea where sea water temperature ranges from 14-18 °C.

First of all, I checked the data for consistency just like the example of the blue whale in the add my pet document. If we take the length in cm and multiply it with the WW measurements of a hatchling and an adult we get the following length per cubic root of weight:

Hatchlings → $0.7*0.15^{-1/3} = 1.32$ cm $g^{-1/3}$
Adults → $24*2800^{-1/3} = 1.7$ cm $g^{-1/3}$

Although this difference is not that big, I think it is to big on such a small number. It appears that hatchlings and adults not exactly have the same shape and composition. This could be explained by the presence of a cuttlebone. According to previous literature, the cuttlebone becomes relatively smaller with growth of the animal and the proportion changes (Denton & Gilpin-Brown 1973).

My second step was to convert the length measurements into volumetric lengths, since DEB works with volumetric lengths instead of shape specific ones. In order to do this we needed the data about WW and physical length. Because the data is a bit inconsistent, I did the calculations for hatchlings and adults separately:

	Hatchling	**Adult**
Wet weight (gr)	0,15	2800
Physical volume (cm ³)	0,15	2800
Physical length (cm)	0,7	24
Shape coefficient	0,759042	0,587275
volumetric length (cm)	0,531329	14,0946

Due to the inconsistency of the data, the shape coefficient also does not correspond between hatchlings and adults.

Another point of discussion arises from the data about reproduction. The reproductive cycle of *Sepia officinalis* is well studied but also very complex. First of all we have the so called "Big-Bang" spawners who spawn just once in their live and most of the time die, directly afterwards. But there is also the possibility of being a intermittent spawner. The difference lies in the duration of egg production. In intermittent spawners this period could last much longer until 1/3 of the life cycle (Laptikhovsky et al. 2003). This has implications for the amount of reserve located to reproduction and the starting point of this event. Big-bang spawners start to produce eggs later but the amount of reserve located to reproduction has to be higher in order to achieve the same potential fecundity.

Secondly, *Sepia officinalis* starts to produce eggs in its juvenile state. If an individual contains eggs smaller than 2 mm it is still considered to be immature but the offset to reproduction has already begun. So maturation and reproduction seem to take place simultaneously. This is in contrast with the standard DEB-model which assumes that when the level of development, represented by the state variable maturity, reaches the juvenile-adult threshold, no more energy is spent on development (Meer van der 2008). Maturity has reached its maximum and from now on the energy is channeled into reproduction. The deviation in development from the DEB assumption should be well considered. Maybe it is necessary to incorporate the special life cycle of the sepia into an alternative model.

A third complication comes from the given that fecundity of the sepia depends on the length of the spawning period and the life span (Laptikhovsky et al. 2003). Both factors are highly variable and depend on temperature (Richard 1971; Forsythe et al. 1994). So, maybe this problem can easily be solved by a temperature correction factor, but then we need to know the exact correlations between the length of spawning period and temperature and between life span and temperature.

Finally I think it is noteworthy that in some sepia there are indications of resorption of oocytes (Laptikhovsky et al. 2003). I see this as an important indication that, in nature, sepias have to deal with long lasting low food conditions during which they are not capable of meeting their daily energy demands. In order to fuel their maintenance needs they start to break down their oocytes for energy.

In my next step I tried to calculate the von Bertalanffy growth rate. I did this with the formula:

Maximum possible age at birth = $L_b * r_B^{-1}$/ultimate length

Maximum possible age at birth is 45 d according to Nixon and Mangold (1998). Volumetric length at birth is 0.53 cm as calculated above. The ultimate length, I don't know precisely what is meant by that. Is it the maximum possible length or the most occurring length of the adult sepia. So calculations are made twice. Once with ultimate length = 14.09 cm and once with ultimate length = 15.18 cm(based on WW = 3500 g and L_w = 40 cm). The von Bertalanffy growth rate then becomes;

45*14.09/0.53 = 1196.32 r_B = 1/1196.32 = 8.359E-4 d^{-1}
45*15.18/0.53 = 1288.86 r_B = 1/1288.86 = 7.759E-4 d^{-1}

I assume that the ultimate length corresponds to the greatest length found in nature. Then we come to a growth rate of 7.759E-4 d^{-1}. This is very low because this would mean that during the two years (730 days) a sepia could only grow 7 cm (L_∞ - (L_∞ -L_b)(exp r_Bt))! If we look at the average volumetric length reached in two years we come to a volumetric length of 14.09 cm. Twice as much as the von Bertalanffy growth rate predicts. So here goes something wrong. Instead of an growth rate of E-4 a growth rate of E-3 is more realistic.

If I could run files in Octave and know how to work with the DEB files than I would be able to put my data about L_b, L_∞, a_b, r_B at f_1 in the file debtool/animal/get_pars_g and obtain the parameters g, k_M = k_J, v, U_{0E}, U_{bE} at f_1. These parameters are only valid for growth at a single food level since we don't have data obtained at various food densities.

If I'm correct I could also insert my data in the mydata_mypet file and get estimations about the energy conductance, digestion efficiency, kappa, reproduction efficiency, maintenance costs etc. And these calculated values I could copy into the pars_mypet file to get that whole list of parameter estimations to which we were introduced on our first meeting with add my pet. I already sent some data about the sepia to you Bas, and you putted them in the mydata_sepia_officinalis file. But there the a_b is 24 days and the a_p is 410 days. According to my data these value have to change toward 45 and 70. I understand that maybe the a_b turns into 24 by a dia pause but then still the 410 days of a_p is way too high. Also, I think the Rm is too high. In this file it is put on 6000/365 but spawning sepia only have a potential fecundity of 3000 eggs. Shouldn't it be 3000/365 then? And I have another data point for sepia of 250 mm ML which contain 365 eggs. Both values are for temperatures of the Aegean sea which I consider to be 16 °C.

My last comment refers to the data about energy uptake and absorption. These measurements are performed by looking at oxygen consumption, growth and energy content of the faeces and the food. They are not related to volume or surface area of the animal his body. So in order to use them in a DEB context they need to be converted into surface and volume specific values.

Finally I want to conclude that, although the data of *Sepia officinalis* is variable among authors, a lot is already know about these animals. I think we can make good parameter estimations with the present knowledge. But the correlation between a lot of characteristics of this animal with temperature need to be well understood. Otherwise you will screw up your estimations and get non representative results.

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