Representation of individual variability in a Dynamic Energy Budget - Individual-based model

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The most natural link between DEB (Dynamic Energy budget) and population models is with individual-based (IB) models which explicitly follow all individuals in a population and preserved the dynamic response of an individual's life history to changes in environment (Jager et al., 2014). In return DEB approach is appropriate as a building block for IB models because it translates environmental conditions to individual performance (growth, survival and reproduction) and it specifies the trade-offs in biological processes and life history traits that DEB specifies (growth vs. reproduction, time and size to maturation) (Martin et al., 2012).

Nevertheless DEB and IB models do not focus both on the same individual. DEB model deals with an average individual that will survive (Kooijman, 2000). IB model tries to capture the variability between individuals acknowledging the individuation principe (DeAngelis and Mooij, 2005; Huston et al., 1988).

The individuation principle is based on two main sources of differences between individuals, (i) genetics pools difference and (ii) past and current interactions with environment (including trophic competition) which depend on individual localisation in the environment (Huston et al., 1988). That leads to two types of coupling between IB and DEB modules : (i) identical DEB parameters but different history between individuals or (ii) different DEB parameters and different history between individuals.

# Review of variability simulation in DEB-IB model

In the first type of coupling (identical DEB parameters but different history), we found the Alver et al. (2006) approach. These authors introduced variability only by considering differences in the initial states variable distribution. To this end, they created an initial population by spinning up the model with a large population subjected to varying feeding conditions. At the moment when the egg ratio was similar to the average initial egg ratios of the experimental populations, the simulation was stopped, and the state values of a random selection of 100 different super individuals were used to initiate the test population (Alver et al., 2006).

Saraiva et al. (2014) simulated mussel physiology based on a DEB approach without any individual variations of parameters. Interactions for food and processes at the population level (egg mortality, background mortality) only made differences in the simulated population dynamics. A similary approach was developed for the anchovy population dynamic by Pethybridge et al. (, 2013). In that application, all population simulations were initialised with a cohort consisting of a one yolk-sac larvae and a spin-un run of 5 years was performed

Beaudouin et al. (2015) used the same DEB parameters for all the individuals of the simulated zebrafish population. Variability was introduced by random draws of initial length, initial energy density and eggs number for female adults.

In the second type of coupling (different parameters between individuals), the selection of fluctuating parameters introduces subdivisions between approaches. The first attempt was proposed by Kooijman et al. (1989). The stochasticity was introduced in two ways : (i) in food gathering with a decision to feed based on a Poisson process or (ii) with a single multiplicative log-normally distributed scatter for all the parameters but for size-specific costs for growth, maintenance and the partition coefficient. The introduction of theses individual variations prevented death by starvation at the take over by the new generation. Moreover, each generation went extinct only halfway through the period of the next generation and the amplitude of the population oscillations was significantly reduced.

Kooijman (2009) proposed an interesting simulation of social interactions of gouramis fish in rearing tanks with similar DEB parameters between individuals. First stochasticity was introduced through the random location of appearing food particles which leads to different travel times for a fish. Second, social interactions were simulated by making food particle invisible for some fish according their relative size.

Bacher and Gangnery (2006) in their simulation of oyster populations dynamics assumed that variability would only affect the half-saturation coefficient  $K_x$ . Simulating variable growth trajectories with normal-distributed values of  $K_x$  reproduced well observed standard deviations of fresh tissue mass. On the whole, the results confirmed that individual variability attenuated the dramatic changes of stock and harvested production curves due to rapid oyster growth during spring, but did not modify the shift between the harvested productions.

Thomas et al. (2016) introduced inter-individual DEB variability in their simulation of invasion of Pacific oyster through: (i) an individual initial state computed according to the initial oyster length and fry flesh mass distributions, and (ii) a specific half-saturation coefficient of the assimilation function response  $K_x$  drawn from a Gaussian distribution (as in Bacher and Gangnery, 2006).

Beaudouin et al. (2012) used calibration results to initialise parameters variability of the population in DEB-inspired model for the midge. It is worthwhile notice that some parameters (individual components of maximal length and growth) were inherited from one generation to the next.

In the generic approach of Martin et al. (2013), individuals have a lognormally distributed scatter multiplier that affects the maximum surface area specific assimilation rate,  $\{\dot{p}_{Am}\}$  and, indirectly in the scaled DEB model, the maximum surface-area-specific ingestion rate,  $\{J_{XAm}\}$ ; the half-saturation coefficient, K; and the energy investment ratio, g and the scaled reserves at birth

 $U_E^b$  and at puberty  $U_E^p$ . Parameterisation revealed that the the energy investment ratio, g and the energy conductance  $\dot{v}$  positively covaried and their ratio was well determined. An analog approach were performed by Galic et al. (2017) for the simulation of Gammarus population dynamics.

As a conclusion of this rapid review, I retain that

• the assimilation process, in its behavioral aspect or in its quantification through parametrisation, has received the most attention to introduce variability in IB approach

• the "degree of freedom" of the DEB variability is very restricted. In most applications, only one single scatter is used.

These conclusions are probably the result of a sensible modelling practice where the modeller tries to respect the parcimony principle and to keep his model trackable. That does not prove that the reality is so simple. But the solution where all processes parameters are randomly drew is attractive because of its parallelism with (supposed, suspected) individual variability of physiological responses, but is limited by the small amount of information on such variability (Bacher and Gangnery, 2006).

### Why I imagine to need more DEB variability?

Part of my research deals with the populaton dynamics of the European sturgeon, a critically endangered, long-lived diadromous fish. We finished a first implementation of a DEB-IB model (Vaugeois et al., n.d.) to explore what triggers the downstream migration. We used the now-usual approach of Martin et al. (2013) with a log-normal scatter on  $\{\dot{p}_{Am}\}$ . The next applications will be dedicated to simulate experiments which were performed in mesocosms with embryos and larvae or 4-month juveniles to test possible effects of temperature, hypoxia and multi-contaminants stress.

The first step is to be able to reproduce, the inter-individual variability not only of length and weight but also of mortality, hatching, and malformation rates for embryos and respiration rate for 4-month juveniles in control experiments (optimal temperature, normoxia and no contamination). This will be a kind of validation of the trigger(s) used in the IB model.

# Alternative solutions of scattering

I propose to test 3 alternative ways to introduce scattering in a DEB-IB approach.

#### scatter more DEB parameters

Given the example of a sturgeon I assume that a species is "ecologically" defined by the its timing of development (age at weaning, late maturity, long-lived) and its large maximum length. So I propose to fix  $E_H^b$ ,  $E_H^p$  and  $L_m$  to the calibration values and make parameters directly related to the physiological machinery  $[\dot{p}_m]$ ,  $\kappa$ ,  $\dot{v}$ ,  $[E_G]$ , in addition to  $\{\dot{p}_{Am}\}$ , variable between individuals. Since the maximum length is a compound parameter, the scatter for  $\kappa$ ,  $\{\dot{p}_{Am}\}$  and  $[\dot{p}_m]$  are constrained by the formulae  $L_m = \kappa \{\dot{p}_{Am}\}/[\dot{p}_M]$ .

Probably  $\kappa_R$  should also vary but I postpose this question since the present work is focusing on immature fish in the IB model.

#### Variability of offspring's DEB parameters

DEB theory states that the energy density of offsprings at birth is equal to the energy density of the mother at egg production (Kooijman, 2010). In an IB perspective, I simply propose to calculate the initial energy of embryo with the mother's DEB parameters. Due to the scattering of DEB parameters for the offsprings, some of the embryos will not reach the maturity threshold at birth and will die before starting to feed. The comparison of this mortality rate with mortalty recorded during control experiments will help to calibrate the scattering. It also will be interesting to compare the DEB parameters' distribution between fecundation and birth times to highlight how the DEB machinery induces a kind of selection and introduces some trade-off (correlations) between parameters.

The embryo malformation rate seems to me not easily simulated in the standard DEB. One way may be to use the auxiliary theory of aging (Kooijman, 2000) with the problem of huge density of damage in individual with a very small volume as an embryo.

# Thermal temperature response as a source of variability

The first idea is to simply scatter the 6 parameters around the reference value.

Coming back to Sharpe and DeMichele (1977) one can find that

$$T_{A} = \Delta H_{A}^{\neq}/R \text{ and } T_{ref} = \frac{\Delta H_{A}^{\neq}}{\Delta S_{A}^{\neq}}$$
$$T_{AL} = -\Delta H_{L}/R \text{ and } T_{L} = \frac{\Delta H_{L}}{\Delta S_{L}}$$
$$T_{AH} = \Delta H_{L}/R \text{ and } T_{H} = \frac{\Delta H_{H}}{\Delta S_{H}}$$

where *R* the gas constant which is physical constant,  $\Delta H_A^{\neq}$  the enthalpy of activation in J mol<sup>-1</sup>,

 $\Delta H_L$  and  $\Delta H_H$  the changes in enthalpy of the low and high temperature inactivation in J mol<sup>-1</sup>,  $\Delta S_A^{\neq}$  the entropy of activation in J mol<sup>-1</sup> K<sup>-1</sup>  $\Delta S_L$  and  $\Delta S_H$  the change in entropy of the low and high temperature inactivation in J mol<sup>-1</sup> K<sup>-1</sup>, which are constants which reflect the individual thermodynamic characteristics of the organism's control enzyme system which is assumed to control development (Sharpe and DeMichele, 1977).

These equations show that the fluctuations of 6 Sharpe's parameters are not independent. The parameters' scattering has to take into account of these relations.

It is likely that the maintenance costs of an individual with a larger thermal tolerance will be higher that an other with a more restricted range. My guess is that a (small) proportion of  $[\dot{p}_T]$  is proportional somehow to the 3 enthalpies and entropies (or to some of them). But a biochemical ground is needed before being able to integrate this feed-back in the DEB equations.

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