

## Appendix S1

### Generalized DEB model structure

This section will describe some basic features of a standard DEB model (for deeper discussions of the fundamentals behind the theory see [1,2]). Standard versions of DEB models conceptually discriminate between the state variables energy reserve,  $E$  (J), structural volume,  $V$  (cm<sup>3</sup>), and maturation,  $E_H$  (J). Once the threshold of puberty has been reached, the state variable reproductive buffer,  $E_R$  (J), can be included. Reproductive buffer accounts for variability in the reproductive potential of mature individuals. The mass of an organism at any given point in time is defined by the contributions from reserve, structure, and reproductive buffer. Maturation, in turn, is understood as energy or mass that dissipates in the form of heat or metabolites as the organism increases its maturity; therefore, this state variable does not contribute to total mass. A chief assumption in standard DEB models is that the biochemical composition of reserve and structure are constant (i.e. strong homeostasis assumption). Although the state variables cannot be measured directly, their dynamics are fully described by a set of equations that will ultimately characterize an organism's physiological condition [3].

Before defining the processes that govern an individual's physiological condition, it is worth elaborating on how DEB theory deals with matters of size and shape. Assuming that the organism's shape does not change with growth (i.e. isomorphy), the model relies on structural length  $L$  (cm), rather than physical length  $L_w$  (cm), to provide a measure of size. Structural length is preferred because (1) it only relates to structural volume discriminating between contributions from

24 other state variables, and (2) it is not affected by the organism's shape, thus favoring  
 25 inter-species comparisons [1]. The DEB parameter shape coefficient  $d_M$   
 26 (dimensionless) serves to translate physical measurements taken from some  
 27 representative length (e.g. arm length) to structural length:  $L = d_M \times L_W$ . In the  
 28 model, structural length defines all physiological processes proportional to area or  
 29 volume. The equations describing surface-area related processes are expressed in  
 30 terms of  $L^2$  (cm<sup>2</sup>), while those proportional to volume are expressed in terms of  $L^3$   
 31 (cm<sup>3</sup>). All rates (units t<sup>-1</sup>) are written with a dot as in  $\dot{p}_A$ . All surface-area specific  
 32 quantities (units L<sup>-2</sup>) are written in curly braces as in  $\{\dot{p}_{Am}\}$ . All volume-specific  
 33 quantities (units L<sup>-3</sup>) are written in square brackets as in  $[\dot{p}_M]$ .

34 Energy reserve changes as the organism acquires food. DEB theory makes  
 35 use of a scaled version of Holling's type II functional response model [4],  $f$   
 36 (dimensionless), to account for the effects of food availability,  $X$  (resource density, 2-  
 37 cm shell length mussels m<sup>-2</sup>), on feeding and assimilation flux. The amount of  
 38 energy entering the body is assumed to be proportional to the surface-area of the  
 39 structural volume, i.e.  $L^2$  (cm<sup>2</sup>). Thus, as the organism forages the energy  
 40 assimilated through the gut,  $\dot{p}_A$  (J d<sup>-1</sup>), can be described by:

$$41 \quad \dot{p}_A = M \cdot \{\dot{p}_{Am}\} \cdot L^2 \cdot f \quad \text{with} \quad f = \frac{X}{X + X_k} \quad (1),$$

42 where  $\{\dot{p}_{Am}\}$  is a DEB parameter known as maximum surface area-specific  
 43 assimilation rate (J d<sup>-1</sup> cm<sup>-2</sup>) and  $M$  is a shape correction function (dimensionless)  
 44 explained in the main text (Eq. 1). The parameter  $X_k$  represents the half-saturation

45 coefficient or Michaelis-Menten constant (resource density at which feeding rate is  
 46 one half of its maximum value) [5]. The process of assimilation is not perfect;  
 47 inefficiencies in transforming energy from food into energy reserve determine that a  
 48 fraction of the available energy is dissipated.

49 The energy stored as reserve is balanced by all the metabolic needs of the  
 50 organism, including growth, development (i.e. maturity), reproduction and  
 51 maintenance (structural and maturity) [6], as well as by the energy dissipated  
 52 through the processes of growth and reproduction. The total energy allocated for  
 53 those needs is known as utilization flux,  $\dot{p}_C$  (J d<sup>-1</sup>). Both the assimilation  $\dot{p}_A$  and the  
 54 utilization  $\dot{p}_C$  fluxes define the dynamics of the reserve  $E$ :

$$55 \quad \frac{dE}{dt} = \dot{p}_A - \dot{p}_C \quad (2)$$

$$56 \quad \dot{p}_C = E \cdot \frac{M \cdot \dot{v} \cdot [E_G] \cdot L^2 + \dot{p}_M}{\kappa \cdot E + [E_G] \cdot L^3} \quad (3),$$

57 where three DEB parameters are introduced; energy conductance,  $\dot{v}$  (cm d<sup>-1</sup>),  
 58 volume-specific cost of structure,  $[E_G]$  (J cm<sup>-3</sup>), and  $\kappa$  (dimensionless, explained  
 59 below). The equation for estimating  $\dot{p}_C$  has been derived assuming that reserve  
 60 density,  $[E] = E/V$  (J cm<sup>-3</sup>), follows first order dynamics – i.e. the rate of decrease of  
 61 reserve density is proportional to the amount of reserve density [7]. Notably, this  
 62 aspect of DEB theory offers a mechanism for filtering the effects of highly variable  
 63 environmental conditions, thus suiting the organism with a homeostatic capacity. In  
 64 depth explanations of the formal derivation of  $\dot{p}_C$  can be found in Kooijman [1] and  
 65 Jusup et al. [8].

66 The utilized energy is then distributed among the metabolic processes –  
67 somatic maintenance,  $\dot{p}_M$  (J d<sup>-1</sup>), structural growth,  $\dot{p}_G$  (J d<sup>-1</sup>), maturity  
68 maintenance,  $\dot{p}_J$  (J d<sup>-1</sup>), and maturation or reproductive buffer,  $\dot{p}_R$  (J d<sup>-1</sup>) (Fig. 1).  
69 The long-standing problem of allocation has been solved by DEB theory via the so-  
70 called *kappa* ( $\kappa$ ) rule [1,9]. The parameter  $\kappa$  amounts to a fixed fraction of energy  
71 utilized from the reserves that goes to somatic maintenance and growth, the former  
72 having absolute priority over the latter. For ectothermic organisms, somatic  
73 maintenance amounts to the energetic costs associated with the turnover of  
74 structural proteins and the maintenance of metabolite concentration gradients  
75 across cell membranes. Since all these costs are proportional to structural volume,  
76 somatic maintenance can be described by:

$$77 \quad \dot{p}_M = [\dot{p}_M] \cdot L^3 \quad (4),$$

78 where  $[\dot{p}_M]$  is a parameter known as volume-specific somatic maintenance cost (J d<sup>-1</sup>  
79 cm<sup>-3</sup>). Due to the priority given to somatic maintenance, the energy derived to  
80 structural growth can be calculated from  $\dot{p}_G = \kappa \cdot \dot{p}_C - \dot{p}_M$ . Growth is understood as  
81 a change in structure (excluding dynamics in body size due to fluctuations in energy  
82 reserve and reproductive buffer), which can be described by [8]:

$$83 \quad \frac{dL}{dt} = \frac{1}{3 \cdot L^2} \cdot \frac{\dot{p}_G}{[E_G]} \quad (5).$$

84 Note that equation 5 includes the parameter volume-specific cost of  
85 structure  $[E_G]$  to account for the cost of converting energy from reserve to  
86 structure (including tissue production and anabolic overheads). This formulation is  
87 equivalent to the traditional von Bertalanffy growth equation [10], whose

88 parameter von Bertalanffy growth coefficient,  $\dot{r}_B$  ( $d^{-1}$ ) describes the decreasing rate  
 89 at which individuals reach their ultimate size  $L_{\infty}$  resulting from the balance  
 90 between food assimilation and somatic maintenance [6,7]. Furthermore, this  
 91 mechanism is incorporated in DEB theory's formulation for this parameter;

92 
$$\dot{r}_B = \frac{1}{3} \cdot \left( \frac{[\dot{p}_M]}{\kappa \cdot f \cdot [E_m] + [E_G]} \right)$$
. The validity of this formulation has been confirmed by

93 successfully modeling the growth trajectories of many taxa reported in the  
 94 literature [see 1 for details].

95 The utilized energy not going to somatic maintenance and growth,  $\dot{p}_C \cdot (1 - \kappa)$   
 96 , is channeled to cover costs of maturity maintenance,  $\dot{p}_J$ , and either increase the  
 97 level of maturity or fill up the reproductive buffer,  $\dot{p}_R$ ; energy allocated to  
 98 maturation is assumed to increase from the age at birth until puberty, after which  
 99 the available energy is directly used for building-up the reproductive buffer (Fig. 1).  
 100 Maturity maintenance,  $\dot{p}_J$  ( $J d^{-1}$ ), which accounts for the maintenance of increased  
 101 complexity attained throughout development, is assumed proportional to the level  
 102 of maturity and can be modeled by:

103 
$$\dot{p}_J = \dot{k}_J \cdot E_H \tag{6}$$

104 where the parameter  $\dot{k}_J$  represents the maturity maintenance rate coefficient ( $d^{-1}$ ).

105 Once puberty is reached ( $E_H \geq E_H^p$ ), maturity maintenance becomes constant.

106 Knowing the energy allocated to maturity maintenance, the dynamics of  $\dot{p}_R$  can be  
 107 tracked through:

108 
$$\dot{p}_R = \dot{p}_C \cdot (1 - \kappa) - \dot{p}_J \tag{7}$$

109           While  $\dot{p}_R$  is equivalent to the rate of change of the maturation state variable  
110 (i.e.  $dE_H/dt$ ) before puberty, it describes dynamics of the reproductive buffer state  
111 variable (i.e.  $dE_R/dt$ ) after puberty is reached. Gonadal tissue is then synthesized  
112 from the reproductive buffer. The efficiency of turning reserve energy into eggs or  
113 sperm is determined by a reproductive efficiency coefficient  $k_R$ . We refer to the  
114 maturation state variable to determine the level of maturity at any given point in  
115 time, as well as the timing of transitions between developmental stages. Explicitly  
116 relying on the state variable maturation liberates the model from having to use size  
117 as a metric for developmental stage. This feature is particularly relevant for species  
118 that can grow or shrink indeterminately, such as sea stars (Feder, 1956; Sebens,  
119 1987).

120           Physiological rates are temperature-dependent, and need to be corrected  
121 accordingly. DEB models make use of the Arrhenius relationship to describe the  
122 influence of body temperature on physiological rates over the range of  
123 temperatures where enzymes can be assumed to be active, delimited by the  
124 parameters  $T_L$  (K) and  $T_H$  (K). The parameter  $T_A$ , known as Arrhenius  
125 Temperature, allows capturing the thermal-sensitivity of the organism within these  
126 margins. Above and below the thermo-tolerance window enzymes become inactive,  
127 leading to a decline in physiological rates, which can be traced by the parameters  
128  $T_{AL}$  and  $T_{AH}$ , respectively [11,12]. These five parameters fully define an organism's  
129 thermal performance curve, in accordance to the formula:

$$130 \quad \dot{k}(T) = \dot{k}_1 \cdot \exp\left\{\frac{T_A}{T_1} - \frac{T_A}{T}\right\} \cdot \left(1 + \exp\left\{\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right\} + \exp\left\{\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right\}\right)^{-1} \quad (8),$$

131 where  $\dot{k}(T)$  is the value of the physiological rate at a given body temperature  $T$  (K),  
 132 and  $\dot{k}_1$  is the known value at a reference temperature  $T_1$  (K).

133 Finally, DEB models explicitly acknowledge the existence of overhead costs  
 134 associated with processes where energy-conversion inefficiencies between different  
 135 compartments are observed. Such overhead costs, linked to assimilation, growth,  
 136 and reproduction (Fig. 1), translate to energy losses in the form of heat and  
 137 metabolites [1].

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### 139 **Appendix S1 References**

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