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The Basic Dynamic Energy Budget Model and Some Implications

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Abstract

Dynamic energy budget models are the most ambitious of resource allocation models in biology, with many practitioners claiming that they apply to all organisms with only a few changes in parameters. Because of this generality, they make very broad predictions about how organisms function. There is extensive literature on the topic, but some of the broad implications nevertheless remain largely unexplored. In this paper, we present a careful derivation of the basic version of the model from elementary biological assumptions, and we identify some of the important implications of the model for growth, starvation, maturation, and reproduction.

Keywords: dynamic energy budget modeling, organism growth, starvation

1 Introduction

The formal DEB theory of dynamic energy budget modeling dates from seminal work by Sebastiaan A. L. M. Kooijman [1], which presented the basic structure that has been retained in DEB modeling. Kooijman has been a prolific author and has trained a large number of researchers, thereby creating a large community dedicated to modeling based on the formal theory. More generally, any other models that attempt to account for resource flow in animals, such as the net production model [4], ought to be classified under the general heading of dynamic energy budget models, although some practitioners of DEB theory believe that the term “dynamic energy budget” should be used only in the narrower confines of the formal theory.

There has been little integration of dynamic energy budget models into the larger context of ecology, where there are opportunities to connect models of individual organisms to models of food webs and other communities. The broader community of ecological modelers has not incorporated DEB theory into its repertoire of techniques. A possible reason for this lack of enthusiasm by ecological modelers is the way the theory has been presented. There are a number of survey papers that contain semi-mechanistic derivations of the basic equations of DEB theory, in which a key point is assumed without clear justification. The careful reader of these papers may well get the impression that the theory is somewhat ad hoc, which it is not. Kooijman’s development of the theory is fully mechanistic, with all assumptions given a biological justification [2]. Another difficulty related to the presentation of DEB theory is the relative impenetrability of the standard symbol set. There are two common symbol sets, depending on whether the currency used for the model is actually energy or is instead some other limiting quantity such as total mass or moles of carbon. Both of these systems, however, use notation for important quantities that incorporates symbols normally reserved in mathematics for delimiters, and the symbol e, normally reserved by mathematicians for

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the base of the exponential function, is commonly used as a state variable. These notational quirks make it difficult for a person not already well versed in the theory to understand the equations.

The purpose of this paper is to present a careful derivation of the standard DEB model that raises questions about some details and presents some general properties of the standard model that are independent of organism. My derivation is essentially that of Kooijman, but with a simplified symbol set that is independent of the choice of currency for the model. It is hoped that the reader will come to understand the promise of DEB theory as a tool for ecological modeling. To help the reader understand the primary literature, formulas that connect the simplified notation of this paper to that used by Kooijman [2] are presented in Appendix A.

2 Development of the Model

Dynamic energy budget (DEB) models describe the life history of an organism in terms of a small number of variables that represent the organism's state as it changes over time, together with a small number of fundamental processes that describe the mechanisms responsible for changes in the state variables. The same model can be used for a variety of species and environments merely by changing the values of a small number of primary parameters. The simplest DEB model is for animals that exhibit indeterminate growth and maintain the same shape, relative proportions, and structure from birth. The model has been extended to more complicated animals, but here we consider only the simplest version.

The key idea of DEB models is that changes in the amounts of resources invested in various components of an organism are determined by quantifiable biological processes. Any conserved quantity, such as energy or moles of carbon atoms, can be used for the currency in the model. The standard notation for DEB models is different depending on the choice of currency and commonly uses volume, rather than the common currency, as a measure of one of the state variables, which introduces the need for conversion factors. The notation presented here does not depend on the choice of currency, which will be referred to euphemistically as 'energy' (with the quotation marks). Capital letters are used for the original variables in the model, with the corresponding lower-case letters used for their dimensionless versions. Lower-case Greek or Latin letters are used for the physiological parameters in the dimensionless model.

2.1 State Variables

The basic dynamic energy budget model includes four state variables. These quantities are distinguished by function rather than structure, so they are not directly observable in a given organism.

Structure (W) refers to the corporeal material of an organism that contributes directly to the animal's ability to collect and process resources. Structure contributes only indirectly to reproduction through the resources it is used to collect. It requires maintenance, which is an expenditure to replace losses due to metabolic processes.

Reserve (E) refers to any corporeal material that is being stored for future allocation to other components. It does not contribute directly to either resource collection or reproduction, and it does not require maintenance. In a more sophisticated model with multiple resources, each potentially limiting, there needs to be a separate reserve for each resource.

Maturity (H) is a state variable that accounts for 'energy' expended from reserves for the purpose of preparing for reproduction, including 'energy' consumed in the process of reorganization, as when organ systems are built in an embryo, as well as 'energy' invested in permanent reproductive organs. While 'energy' expended for maintenance does not need to be incorporated into a state variable, 'energy' invested in maturity does need to be accounted for since a specific amount of such 'energy' marks the transition from juvenile to adult. Hence, the maturity variable is abstract in the sense that it includes resources that are used without being incorporated into the organism. Maturity requires maintenance, as complexity and reproductive organs can sometimes be sacrificed in response to starvation.

The reproduction component (R) includes 'energy' present in the form of gametes, 'energy' used for gametes that have already been released from the organism, and 'energy' stored specifically for future reproduction. This component does not require maintenance.

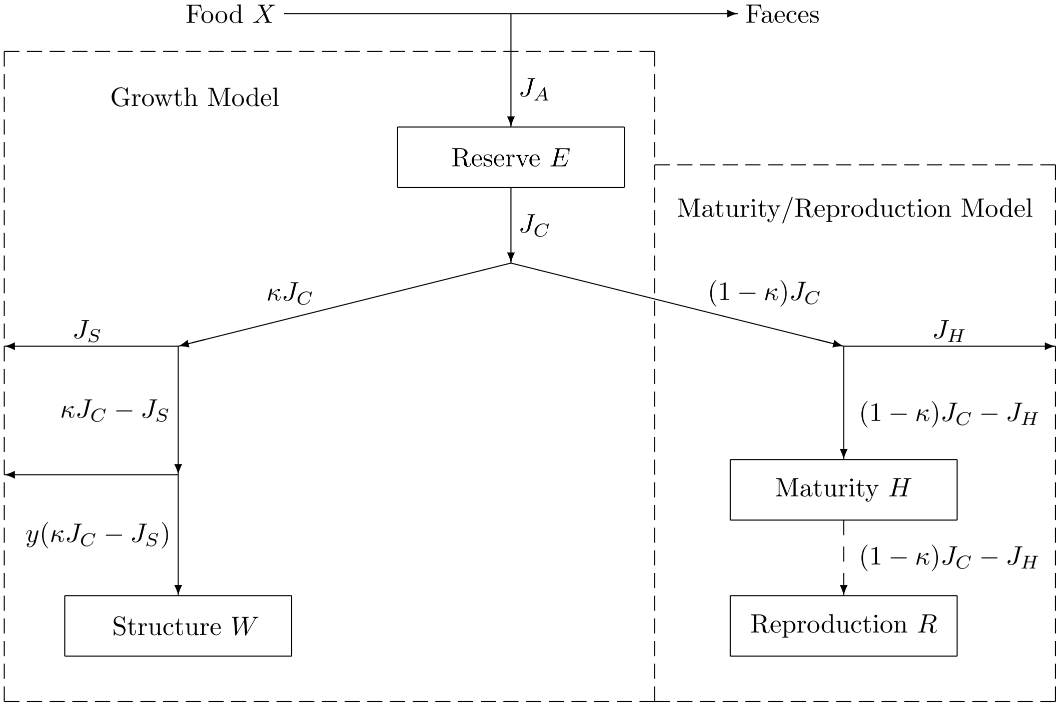

Figure 1: Schematic of a model organism showing state variables and fluxes. State variables are given as 'energy' (energy, mass of carbon, or moles of carbon) and fluxes are given as 'energy' per unit time.

2.2 Processes

The standard DEB model assumes a specific connection pathway for changes among the four components, as shown in Figure 1. 'Energy' is collected from the environment and assimilated into reserve at rate J_A. It is mobilized from the reserve at rate J_C, with the fraction κ allocated for somatic uses and the remaining fraction allocated for maturation or reproduction. Costs J_S and J_H for somatic and maturity maintenance are deducted from the respective streams, with the remainder of the somatic stream going to growth and the remainder of the maturity/reproduction stream going to maturity for a juvenile or reproduction for an adult. 'Energy' allocated to growth must be converted into structure, with the yield in structure a fixed fraction y of the resources invested, and with the remaining investment lost through chemical reactions needed to build the specific tissues that comprise the structure. Since maturity is largely abstract, it can be thought of as having the same composition as reserve; hence, there is no need for a yield parameter. One can include a yield parameter for conversion from reserve to reproduction; here we are thinking of reproduction primarily as reserve that has been allocated for embryos, in which case it has the same composition as ordinary reserve. A subsequent submodel that deals with the conversion of reproductive 'energy' into gametes would then need a conversion factor. Note that each of the fluxes has the dimension ‘energy’ per time, while y has the dimension ‘energy’ incorporated into structure per ‘energy’ of reserve.

2.3 The Growth Model

The growth model consists of the differential equations for structure and reserve along with algebraic equations for the assimilation, mobilization, and somatic maintenance fluxes, which need to be prescribed in terms of the structure variable. Ultimately, it is most convenient to replace the original variables E and W with the reserve density U and structural length L, thereby eliminating the dependence on the choice of currency.

Reserve Density and Structural Length

The differential equations that describe the changes in structure and reserve are given in terms of the standard fluxes as

$$\tfrac{dE}{dt} = J_A - J_C, \tag{1}$$

$$\tfrac{dW}{dt} = y(\kappa J_C - J_S). \tag{2}$$

We replace W by the structural length L and E by the reserve density U, with these defined by

$$W(t) = \Gamma L^3(t), \qquad E(t) = U(t)W(t) = \Gamma U(t)L^3(t), \tag{3}$$

where Γ is the density of ‘energy’ contained in a unit volume of structure. This parameter allows all quantities measured in ‘energy’ to be converted into an equivalent structural length.

After changing variables, the structure equation becomes

$$3\frac{dL}{dt} = \kappa y \frac{J_C}{\Gamma L^2} - y\frac{J_S}{\Gamma L^2}, \tag{4}$$

and the reserve equation becomes

$$W\frac{dU}{dt} + U\frac{dW}{dt} = J_A - J_C,$$

or

$$L\frac{dU}{dt} = \frac{J_A}{\Gamma L^2} - (1+\kappa y U)\frac{J_C}{\Gamma L^2} + yU\frac{J_S}{\Gamma L^2}. \tag{5}$$

Completion of the growth model requires specification of the assimilation and maintenance fluxes in terms of L and a reserve dynamics model that provides an additional equation for J_C.

Assimilation Flux and Reserve Dynamics

Animal feeding models lead to the assumption that assimilation flux is proportional to structural area. Postponing consideration of the feeding model details, we can use this assumption to assert that the assimilation flux is given by

$$\frac{J_A}{\Gamma L^2} = Q, \tag{6}$$

where Q depends only on food availability and not on the state of the organism. Thus, the reserve density equation (5) becomes

$$L\frac{dU}{dt} = Q - \left[(1+\kappa y U)\frac{J_C}{\Gamma L^2} - yU\frac{J_S}{\Gamma L^2}\right].$$

It is convenient to define a function D by

$$D(U,L) = (1 + \kappa y U)\frac{J_C}{\Gamma L^2} - yU\frac{J_S}{\Gamma L^2}, \tag{7}$$

which allows us to write the reserve dynamics equation as

$$L\tfrac{dU}{dt} = Q - D(U,L). \tag{8}$$

This equation looks simple, but it is not complete because D includes the unknown mobilization flux J_C, which must be determined indirectly. Instead of deriving a mechanistic model for J_C and using it to calculate D, we derive a mechanistic model for D and then use (7) to calculate J_C. This is done in two stages, determining first the dependence of D on L and then its dependence on U.

When the food availability is constant, the parameter Q is also constant; in this case, the reserve density achieves an equilibrium given by

$$D(U^*(L,Q),L) = Q.$$

We now make the *weak homeostasis* assumption, which is that the equilibrium reserve density for a given food level does not change as the individual grows. This implies that U^* depends only on Q, so the equilibrium equation is

$$D(U^*(Q),L) = Q.$$

Differentiating with respect to L therefore yields $\partial D/\partial L(U^*(Q),L) = 0$. Now suppose U and L are given. We can then define Q^* by $Q^* = D(U,L)$, which means that $U = U^*(Q^*)$. Hence, we have

$$\tfrac{\partial D}{\partial L}(U,L) = \tfrac{\partial D}{\partial L}(U^*(Q^*),L) = 0,$$

leading to the conclusion that D does not actually depend on L.

The form of the function D is further restricted by the partitioning assumption, which says that the equations must all make sense even when applied to only a fraction of the reserve. This argument is typically applied to the definition of D (7), but the conclusion follows much more easily from examination of (8), now with $D(U)$ rather than $D(U,L)$. Suppose we arbitrarily divide the reserve into two portions with reserve densities $U_1 + U_2 = U$. The total assimilation must be divided among the two portions as well, with $Q_1 + Q_2 = Q$. Then

$$D(U_1) + D(U_2) = \left[Q_1 - L\tfrac{dU_1}{dt}\right] + \left[Q_2 - L\tfrac{dU_2}{dt}\right] = Q - L\tfrac{dU}{dt} = D(U_1 + U_2).$$

Similarly, suppose we consider a fraction θ of the total reserve. Assuming starvation conditions ($Q = 0$) for simplicity, we have

$$D(\theta U) = -L\tfrac{d(\theta U)}{dt} = -\theta L\tfrac{dU}{dt} = \theta D(U).$$

These last two results prove that D must be linear; hence, there is a constant ν, with dimension length per time, such that $D(U) = \nu U$. This parameter is called the *energy conductance*. Similarly, it makes sense to call the parameter Q, also with dimension length per time, the *assimilation conductance*.

The result $D(U) = \nu U$ completes specification of the reserve dynamics by

$$\frac{dU}{dt} = \frac{Q - \nu U}{L} \tag{9}$$

and the mobilization flux by

$$J_C = \frac{\nu \Gamma U L^2 + yUJ_S}{1 + \kappa y U}. \tag{10}$$

Substitution of (10) into (4) yields the final growth equation:

$$\frac{dL}{dt} = \frac{y}{3(1+\kappa y U)}\left(\kappa \nu U - \frac{J_S}{\Gamma L^2}\right). \tag{11}$$

After supplementation by algebraic equations to prescribe the somatic maintenance flux J_S and the assimilation conductance Q in terms of the structure variable L, equations (9)–(11) constitute a complete model to determine L, U, and J_C. These quantities can then be used as known inputs for the maturation/reproduction component of the model.

Biological Analysis of Reserve Dynamics

We need to delve a bit more deeply into the assimilation model to fully understand the reserve dynamics equation (9). Suppose Q_m is the maximum value of the assimilation conductance Q. Using a Holling type 2 functional response for the relationship between assimilation and food density x (scaled by the food density corresponding to assimilation at half the maximum rate), the overall assimilation conductance is

$$Q = Q_m f(x) = Q_m \frac{x}{1+x}. \tag{12}$$

Substituting this equation into (9) gives us the standard form of the reserve energy equation,

$$\frac{dU}{dt} = \frac{\nu}{L}\left(\frac{Q_m}{\nu} f(x) - U\right). \tag{13}$$

Given $f \leq 1$, there is a maximum reserve density defined by

$$U_m = \frac{Q_m}{\nu}. \tag{14}$$

The existence of a mathematical relationship among Q_m, ν, and U_m is problematic in the sense that all three of these quantities—maximum assimilation conductance, energy conductance, and maximum reserve density—seem appropriate to take as primary parameters that are determined independently through natural selection. It has become standard in the DEB literature to take Q_m and ν as the primary parameters, with ν thought of as roughly uniform within a given family of organisms, meaning that the equilibrium reserve density scales with Q_m. We will see that maximum structural length L_∞ also scales with Q_m, so the equilibrium reserve density scales with maximum structural length. The inevitable consequence of this conclusion is that larger species in a related family have larger maximum reserve densities, which seems counter-intuitive. Reserve represents investment of resources in a component that can only improve productivity by later reallocation to structure, in the same way that depositing money into a checking account can only improve income by later reinvestment into something productive. In the financial setting, a larger percentage of holdings maintained as cash is a response to greater unpredictability of future earnings, not a consequence of being a larger company. Intuitively, one would expect natural selection to use a larger maximum reserve density as a hedge against greater unpredictability of food supply. The model can predict this result only if maximum reserve density is a primary parameter.

The derivation of the reserve density equation produces the energy conductance parameter ν from a mathematical argument, with no clear biological argument why energy conductance should be a primary parameter. In principle, there is no difficulty in thinking of Q_m and U_m as the primary parameters, with the energy conductance ν as secondary. Unfortunately, this has its own drawbacks. The relative rate of reserve loss due to starvation is given by (13) with $f = 0$, so can be written as either ν/L or Q_m/LU_m. While it is satisfying to see that larger reserve density increases resistance to starvation in the second form, it is problematic to have the starvation rate dependent on the food intake rate, given that there is no food intake in a starvation scenario. Suppose all food is withheld from two organisms in the same family and with the same initial length. If reserve density is roughly fixed in this family, then the organism from the species with larger maximum size would starve faster than its counterpart in spite of having the same current size and reserve density.

While the choice between ν and U_m as the second primary parameter should be based on biological considerations, it is not obvious which considerations are most important; this issue has not been deeply explored in the literature. There is a third alternative, completely unexplored, which is to omit the weak homeostasis assumption. The partitioning argument would still hold to show that D is linear in U for given L, but we would need additional biological assumptions to determine the dependence of D on L. While this alternative is more complicated, it would allow the energy conductance and maximum reserve density to be independent primary parameters.

Maintenance and Nondimensionalization

Any maintenance based on cell upkeep and respiration, as well as tissue replacement, should be proportional to the structure W, which means it can be taken as proportional to the cube of the structural length L. Similarly, maintenance based on control of internal temperature or osmotic pressure should be proportional to the square of the structural length. Maintenance costs based on movement should be proportional to the total mass of the organism, but this would violate the DEB requirement that reserve have no maintenance needs. Instead, DEB models consider only structural mass in determining cost of movement, which is simply added to the upkeep and respiration costs.[1] Taking all of the components together, we can write the maintenance costs as

$$J_S = \Gamma(kL^3 + k_A L^2). \tag{15}$$

Assuming $k_A = 0$ in the standard model (for ectotherms living on land or in salt water), we can complete the growth and flux equations as

$$\frac{dL}{dt} = \frac{y(\kappa\nu U - kL)}{3(1+\kappa y U)} \tag{16}$$

and

$$J_C = \frac{\Gamma U L^2(\nu + kyL)}{1+\kappa y U}. \tag{17}$$

For nondimensionalization, we select reference quantities

$$U_m = \frac{Q_m}{\nu}, \qquad L_m = \frac{\kappa Q_m}{k}, \qquad t_r = \frac{1}{ky}, \tag{18}$$

where L_m can be identified as the maximum structural length. We then define the scaled reserve density u, the scaled length ℓ, the scaled time τ, and the compound parameter ϕ by

$$u = \frac{U}{U_m}, \qquad \ell = \frac{L}{L_m}, \qquad \tau = kyt, \qquad \phi = \kappa y U_m = \frac{\kappa y Q_m}{\nu}. \tag{19}$$

In terms of these new quantities, with the prime symbol for τ derivatives, the model becomes

$$u' = \frac{f(x) - u}{\phi\ell}, \tag{20}$$

$$\ell' = \frac{u - \ell}{3(1+\phi u)}, \tag{21}$$

$$J_C = \frac{\Gamma\kappa^2 Q_m^3}{k^2} \cdot \frac{1+\phi\ell}{1+\phi u} \cdot u\ell^2. \tag{22}$$

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[1] This is an unimportant discrepancy in most contexts, but it means that strict DEB models cannot be used for questions that require an accounting of the metabolic costs of movement, especially for large organisms that tend to have large reserve densities in the standard model.

The dimensionless growth model (20)–(21) has only two parameters: the food density x and the physiological parameter ϕ, which represents the maximum value (given unlimited food density) of the ratio of the amount of structure that could be produced by immediate full mobilization of storage to the amount of structure currently present. This model is equivalent to the version given by van der Meer [6] except for the latter's use of e in place of my u and $g = 1/\phi$ in place of my ϕ.

2.4 Maturation and Reproduction

We now consider the fraction $1-\kappa$ of the assimilate that is not used for somatic maintenance and growth. This portion is initially earmarked for maturation, which includes 'energy' used for reorganization (and therefore expended) as well as 'energy' converted into reproductive organs. The differential equation for maturity increase is

$$\tfrac{dH}{dt} = (1-\kappa)J_C - J_H,$$

where J_C is given by (22). We assume the maturity maintenance flux is

$$J_H = k_H H$$

and define dimensionless maturity h and dimensionless maturity maintenance coefficient σ by

$$H = \frac{\Gamma\kappa^2(1-\kappa)Q_m^3}{k^3 y} \cdot h, \qquad \sigma = \frac{k_H}{ky}. \tag{23}$$

With these definitions, we obtain the maturation model

$$h' + \sigma h = \frac{1+\phi\ell}{1+\phi u} \cdot u\ell^2, \qquad h(0) = h_b, \qquad h(\tau_p) = h_p, \tag{24}$$

where h_b, the dimensionless maturity level at birth, and h_p, the dimensionless maturity level at puberty, are primary parameters. As a practical matter, we can generally take $h_b = 0$, reflecting the low maturity level at birth. Alternatively, we can think of h_p as the increase in maturity from birth to puberty and neglect the maintenance requirement for maturity accumulated before birth. The puberty time τ_p must be determined from the solution of the initial value problem.

After time τ_p, the maturity level is fixed, except under extreme starvation conditions, and the reproduction is given in dimensionless form by

$$r' = \frac{1+\phi\ell}{1+\phi u} \cdot u\ell^2 - \sigma h_p, \qquad r(\tau_p) = 0. \tag{25}$$

For life history optimization problems, we may write the expected total lifetime reproduction as

$$E[r(\infty)] = \int_{\tau_p}^{\infty} \left[\frac{1+\phi\ell(\tau)}{1+\phi u(\tau)} \cdot u(\tau)\ell^2(\tau) - \sigma h_p\right] S(\tau)\, d\tau, \tag{26}$$

where $S(\tau)$ is the probability of survival to age $t = t_r\tau$.

2.5 Summary

The full dimensionless model needed to determine length, storage, puberty time, and accumulated reproduction consists of equations (20), (21), (24), and (25). Aside from parameters absorbed in the scales, the dynamics are completely determined by physiological parameters ϕ, σ, and h_p, along with the function $x(t)$ that describes the time-dependent food availability. If x is constant, then the reserve density quickly approaches $u = f$, which simplifies the growth equation to

$$\ell' = \alpha(f-\ell), \qquad \alpha \equiv \frac{1}{3(1+\phi f)}.$$

This is the von Bertalanffy equation often used for growth of animals; neglecting the small size at birth, we have the result

$$\ell = f\left(1 - e^{-\alpha\tau}\right). \tag{27}$$

The maturation equation then simplifies to

$$h' + \sigma h = 3f\alpha(1 + \phi\ell)\ell^2 \tag{28}$$

and the reproduction equation to

$$r' = 3f\alpha(1 + \phi\ell)\ell^2 - \sigma h_p. \tag{29}$$

3 Qualitative Behavior of the Model

We now examine some of the qualitative predictions made by the standard model under a variety of circumstances. The focus will be on trying to tease out the significance of the dimensionless parameters ϕ and σ and the response of the model to a variety of food conditions.

3.1 Growth

Figure 2 shows the growth history $\ell(\tau)$ under constant food conditions. Figure 2a illustrates the effect of food availability with moderate storage ratio parameter $\phi = 1$. As seen in (27), the primary effect of assimilation saturation f is on the asymptotic structural length; however, there is an additional effect (through α) of increased food in slowing the approach to the asymptotic length; this would be more pronounced with larger ϕ. Figure 2b shows the effect of the storage ratio, with larger values slowing the approach to the asymptotic length.

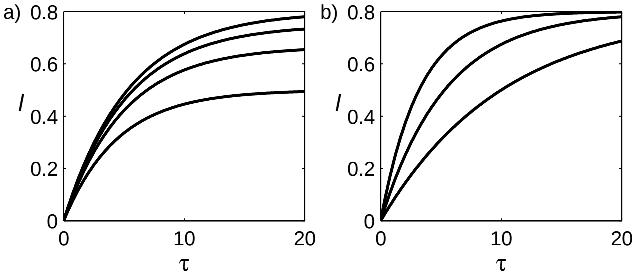

Figure 2: Growth history under constant food conditions: (a) $x = 1, 2, 3, 4$ (bottom to top) with $\phi = 1$; (b) $\phi = 0.1, 1, 4$ (top to bottom) with $x = 4$.

3.2 Starvation

Suppose an animal is initially placed in an optimal environment ($f \to 1$), allowed to grow to a size ℓ_0, and then placed in an environment with no food. It can survive for a time because its reserve can continue to pay maintenance costs even without replenishment. Animals are not capable of more than a miniscule decrease in structural length, so the organism dies shortly after it becomes unable to cover its maintenance costs (see [5], for example).[2] This does not require the reserve to drop to 0 (which in theory takes infinite time), but merely to drop low enough that the model predicts negative growth. From (21), this occurs when

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[2] More sophisticated responses to starvation are also possible; see [2], p. 114–124.

$u = \ell$. Thus, we can define the dimensionless maximum starvation time[3] $\tau_s(\ell_0, \phi)$ by the problem

$$u' = -\frac{u}{\phi \ell}, \qquad \ell' = \frac{u - \ell}{3(1 + \phi u)}, \qquad u(0) = 1, \qquad \ell(0) = \ell_0, \qquad u(\tau_s) = \ell(\tau_s). \tag{30}$$

In general, this problem has to be solved numerically, but the starvation time can be approximated analytically for small ϕ, with the result (see Appendix B)

$$\tau_s \approx \phi F(\ell_0), \qquad F(\ell_0) = \ell_0 \ln \frac{1}{\ell_0}. \tag{31}$$

This result indicates that τ_s/ϕ should be independent of ϕ for ϕ small enough. Figure 3 shows that this conclusion is approximately true even for moderate values of ϕ. Note that Figure 3 makes a prediction that could potentially be tested by experiment: for any given species, individuals that are at roughly 35-40% (corresponding to the theoretical minimum $\ell_0 = 1/e$ of F) of the maximum structural length should be more resistant to starvation than larger or smaller individuals.

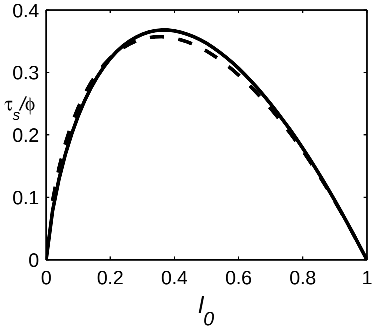

Figure 3: Dimensionless starvation time scaled by ϕ: $\phi \to 0$ (solid), $\phi = 4$ (dashed).

In dimensional quantities, the starvation time is

$$t_s = \frac{L_0}{\nu} \cdot \ln \frac{\kappa Q_m}{k L_0} = \frac{L_0 U_m}{Q_m} \cdot \ln \frac{\kappa Q_m}{k L_0}, \tag{32}$$

depending on the choice of ν or U_m as a primary parameter, where L_0 is the structural length when food is cut off. The second result conflicts with the expectation that starvation time should be largely independent of Q_m. The latter is a measure of the animal's capacity for assimilating food, which should not make any difference to an animal that has no food to assimilate. The result (32) is the principal argument for taking ν rather than U_m to be primary.

If we neglect the subtleties of mobilization and growth, we can make a naive estimate of starvation time. Given that initial food supply is at its maximum, the total amount of reserve 'energy' when food is cut off is

$$E_0 = \Gamma U_m L_0^3.$$

Assuming no further growth, the rate of somatic maintenance, from (15), is $\Gamma k L_0^3$. Given that only a fraction κ of E_0 is available to pay somatic maintenance costs, this means that the reserve energy should last to time

$$\bar{t}_s = \frac{\kappa U_m}{k},$$

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[3] It is the maximum starvation time because a lower initial food concentration would mean a lower initial energy reserve and less time until $u = \ell$.

which is independent of structural length. The actual starvation time should be less than this quantity, which we can check against the time t_s by choosing the structural length corresponding to maximum starvation time:

$$t_s(L_0) \leq t_s\left(e^{-1}L_m\right) = e^{-1}\bar{t}_s.$$

The restrictions of reserve dynamics mean that starvation happens significantly faster than it would if reserve could be used to pay maintenance costs instantaneously.

3.3 Maturation

The parameter σ represents the relative cost of maturity maintenance as compared to that of somatic maintenance. It has two important effects, one of which is on the size achieved at maturity. The value $\sigma = 1$ represents a situation where food shortages affect growth and maturation equally, which means that it takes longer to reach the adult stage but that the size achieved at maturity is unchanged. Many authors have made this simplifying assumption in order to equate maturation with a size and avoid having maturity as a state variable. However, there are many examples of species for which the size at maturity can be highly dependent on food availability. In these cases, it is the underfed individuals that mature at a smaller size; hence, $\sigma < 1$. These features are illustrated in Figure 4, which shows plots of $\ell(\tau)$ against $h(\tau)$ using a representative value of $\phi = 1/3$, high and low food densities, and three values of σ. In both parts, the top curve is for $\sigma = 1$; these curves are identical because low food slows maturation as much as it slows growth, but the low food curve ends at the maximum values of h and ℓ. Smaller values of σ mean that low food slows growth more than maturity, so the curves are pushed down from Figure 4a to Figure 4b.

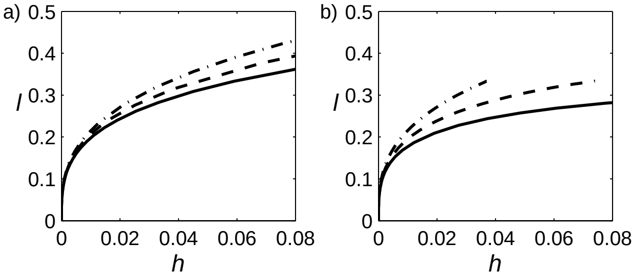

Figure 4: Development curves in the maturity-length phase plane, with $\sigma = 0$ (solid), $\sigma = 0.5$ (dashed), and $\sigma = 1$ (dot-dash): a) $x = 4$; b) $x = 0.5$, both with $\phi = 1/3$.

3.4 Reproduction

A second effect of maturity maintenance is to impose a minimum rate of 'energy' mobilization to maintain status as a reproductive adult. This phenomenon has been observed and is the biological justification for including maturity maintenance in the model. The condition that maturity maintenance for an adult can be paid requires

$$\sigma h_p < \frac{1+\phi\ell}{1+\phi u} \cdot u\ell^2,$$

which corresponds in dimensional terms to

$$k_H H_p < \Gamma(1-\kappa)UL^2(\nu + kyL), \tag{33}$$

given that U is small under starvation conditions. This should be interpreted as a limit to how low the reserve density U can be to avoid regression.

While it is not clear that natural selection acts on a genome to achieve optimal fitness, this assumption is at least plausible. In principle, it can be tested by using dynamic energy budget models to predict optimal parameter values under known environmental conditions. A simple calculation provides a rough estimate of the optimal value of the allocation parameter κ. Equation (27) shows that the dimensionless reproduction rate does not depend directly on κ. This means that the primary effect of κ occurs in the scale, which is the same as for H. We can say that reproduction rate of an adult is roughly proportional to $\kappa^2 - \kappa^3$, which has its maximum at $\kappa = 2/3$. Of course what really matters is the total lifetime reproduction, and this depends on survival rates. The guarantee of a finite lifespan suggests that there is an advantage to earlier maturation, which would be achieved by making κ a little smaller. On the other hand, many organisms live in an environment where the primary cause of death is predation on juveniles, and this suggests that κ should be larger. Reported values of κ are in the range 0.65 to 0.8, which is consistent with these theoretical observations.

Appendix

A. Notation Dictionary

Table 1 presents the important notation for the basic DEB model in its current standard version, along with the equivalents using the notation presented in this paper. The extra factors of Γ in the equivalent notation are because the notation used here is independent of currency. Standard DEB models that use currency other than energy use different notation.

Table 1: Comparison with the standard notation [2].

Standard	Equivalent	type	specifics
L	L	state variable	structural length
$[E]$	ΓU	state variable	energy per unit structural volume
e	u	state variable	dimensionless energy density
$\dot{p}_S$	J_S	flux	somatic maintenance flux
$\dot{p}_A$	J_A	flux	assimilation flux
$\{\dot{p}_A\}$	ΓQ	flux	assimilation flux per unit area
$[E_G]$	Γy^{-1}	parameter	energy cost per unit volume of structure
$\{\dot{p}_{Am}\}$	ΓQ_m	parameter	maximum assimilation flux per unit area
$[\dot{p}_m]$	Γk	parameter	maintenance energy cost per unit volume
$[E_m]$	ΓU_m	parameter	maximum reserve energy per unit volume
ν	ν	parameter	energy conductance
g	ϕ^{-1}	parameter	energy investment ratio

B. Asymptotic Analysis of the Starvation Problem

We begin by rescaling the time in (30) using the substitution

$$\tau = \phi \ell_0 \eta,$$

which changes the problem to

$$\frac{du}{d\eta} = -\frac{\ell_0}{\ell} u, \qquad \frac{d\ell}{d\eta} = \phi \frac{u - \ell}{3(1 + \phi u)}, \qquad u(0) = 1, \qquad \ell(0) = \ell_0, \qquad u(\eta_s) = \ell(\eta_s).$$

Given $\phi \to 0$, we see that length is constant to leading order, which yields the approximate problem

$$\ell = \ell_0, \qquad \tfrac{du}{d\eta} = -u, \qquad u(0) = 1, \qquad u(\eta_s) = \ell_0,$$

with solution

$$\eta_s = \ln \frac{1}{\ell_0}.$$

Thus,

$$\tau_s = \phi \ell_0 \ln \frac{1}{\ell_0},$$

which confirms (31).

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