The bijection from data to parameter space with the standard DEB model quantifies the supply–demand spectrum

Konstadia Lika, Starrlight Augustine, Laure Pecquerie, Sebastiaan A.L.M. Kooijman

HIGHLIGHTS

- We present the bijection between data and parameter space for the standard DEB model.
- The boundaries of these spaces involve a new metric: the supply stress.
- This metric quantifies the supply–demand spectrum for animal species.
- Parameters from 300 species show that invertebrates and ray-finned fish are supply species.
- We explain why birds and mammals up-regulate metabolism during reproduction.

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ABSTRACT

The standard Dynamic Energy Budget (DEB) model assumes that food is converted to reserve and a fraction $\kappa$ of mobilised reserve of an individual is allocated to somatic maintenance plus growth, while the rest is allocated to maturity maintenance plus maturation (in embryos and juveniles) or reproduction (in adults). The add_my_pet collection of over 300 animal species from most larger phyla, and all chordate classes, shows that this model fits energy data very well. Nine parameters determine nine data points at abundant food: dry/wet weight ratio, age at birth, puberty, death, weight at birth, metamorphosis, puberty, ultimate weight and ultimate reproduction rate. We demonstrate that, given a few other parameters, these nine data points also determine the nine parameters uniquely that are independent of food availability: maturity at birth, metamorphosis and puberty, specific assimilation, somatic maintenance and costs for structure, allocation fraction of mobilised reserve to soma, energy conductance, and ageing acceleration. We provide an efficient algorithm for mapping between data and parameter space in both directions and found expressions for the boundaries of the parameter and data spaces. One of them quantifies the position of species in the supply–demand spectrum, which reflects the internalisation of energetic control. We link eco-physiological properties of species to their position in this spectrum and discuss it in the context of homeostasis. Invertebrates and ray-finned fish turn out to be close to the supply end of the spectrum, while other vertebrates, including cartilaginous fish, have stronger demand tendencies. We explain why birds and mammals up-regulate metabolism during reproduction. We study some properties of the bijection using elasticity coefficients. The properties have applications in parameter estimation and in the analysis of evolutionary constraints on parameter values; the relationship between DEB parameters and data has similarities to that between genotype and phenotype.

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1. Introduction

Energetics, i.e. resource acquisition and use of individual organisms, is basic to behaviour, population and ecosystem dynamics and evolution (Sousa et al., 2010). The actual performance of individuals very much depends on environmental factors, the most important being temperature and resource
availability. That is why the potential energetic performance of species can best be compared on the basis of parameter values of a model for this energetics (Kooijman et al., 2008). Dynamic Energy Budget (DEB) models (Kooijman, 2010) are such models for which its applicability to data has been demonstrated in many studies (Pecquerie et al., 2010, 2012; Kooijman, 2013; Kooijman and Lika, 2014a). The model is based on simple thermodynamic principles (Sousa et al., 2006) and applies to all species (micro-organisms, plants, and animals). Animal energetics is well-captured by the standard DEB model (see Appendix A for a summary), which has just a single reserve and structure. This is demonstrated by the add_my_pet collection of data and parameters of over 300 animal species from most larger phyla, and all chordate classes: this model fits energy data very well. The mean FIT mark is 8.4 on the range from minus infinity to 10 (Lika et al., 2011); it stands for 10 times one minus the mean relative error of the various data sets.

Data availability is always a problem for application of elaborate models, certainly for the purpose of comparing a large number of species on the basis of their parameter values. Very little is known about most species. The types of data include uni-variate data, such as body weight as function of time, length, or function of body weight, respiration as function of length, clutch size as function of body weight as well as zero-variate data (data points if you like), such as age at birth, weight at puberty, and length at death. The coupling of traits (feeding, growth, reproduction, and ageing) is key to energetics, implying the necessity to estimate all parameters from all data simultaneously in a single-step procedure (Van der Meer, 2006). While no parameter from a multi-parameter model can be estimated from a single zero-variate data point, parameters might be estimated from a set of different types of zero-variate data. The add_my_pet collection has over 100 different types of data in total, but for any individual species a very limited selection is available. The completeness of data that is available to estimate DEB parameters is scored from 0 (maximum body weight only) to 10 (all aspects of energetics are fixed by data) (Lika et al., 2011); the mean completeness level is 2.5, the maximum one is 6, which illustrates the problem of lack of data even for the best studied species. Kooijman et al. (2008) study the problem of which measurements, or observations if you like, determine which parameters of the standard DEB model. It turned out that particular compound parameters, i.e. simple functions of parameters that have simple dimensions, are much easier to estimate from data than the parameters themselves. Since comparisons between species are most informative if done on the basis of all primary parameters, rather than some compound ones, the covariation method (Lika et al., 2011, 2011) has been worked out to estimate all primary parameters from data. This method uses a selection of parameters for a generalised animal as data points. The generalised animal is a hypothetical animal with a maximum structural length of 1 cm that has typical (i.e. frequently encountered) body-size corrected parameter values (Kooijman, 2010, Table 8.1). The use of (some) parameters of the generalised animal as data points still allows for a difference between estimated parameter values and those of the generalised animal. This method makes sure that data contain enough information to estimate parameters and reduces the risk of arriving at a good fit that makes no physical sense. How well parameters are determined by data generally depends on the combination of values of data and parameters and model structure, a complex problem indeed. Where model complexity and structure can easily be adapted to the needs of available data in descriptive models, they are set by internal logic in mechanistic models like the DEB model and pose conditions for minimal data that is required. Standard statistical procedures (variance–covariance matrices) can be used to quantify uncertainty in parameter estimates in regression situations (added noise in data). A deep problem is that this module for stochasticity is very unrealistic from a biological perspective. Most noise in energy data originates from variability in the environment and in behaviour. DEB parameters are supposed to be individual-specific, so ideally, all data should be from the same individual. The hope is that if data points are means of several individuals, the corresponding parameter set is representative for the species without claiming that they are actually mean values. It is very likely that, in situations where various data sets relate to various populations of individuals, differences in parameter values can be expected. This source of stochasticity easily leads to complex dependencies in data (Bedaux and Kooijman, 1994). We come back to this point in the section on the role of scatter.

This paper aims to study the problem of how well data fix parameters in a new way, working with only a single food availability level (abundant food), a single constant temperature, and data only of the most reduced type: zero-variate data. This in fact corresponds to what is available for most animal species. Even though performance at several food levels is very informative about particular parameters, such data are very hard to obtain and are simply not available in most cases. The add_my_pet collection is presently weak on data on feeding, apart from starving, which doubtlessly reflects the experimental problem of measuring it and the fundamental problem of age and size dependent selection strategies and variations in nutritional values of food types in multi-food type situations. This is why we presently avoid dealing with this complex problem. In view of the many species that sport metabolic acceleration in the collection (Kooijman, 2014), we here include the type M acceleration module (see Appendix A). We also include the ageing module to complete the full life cycle perspective of DEB theory from embryo, juvenile and adult to death by ageing. Although parameter estimation aims to step from data to parameter values conceptually, computationally it makes the inverse step from parameter values to model predictions, where a formalised estimation criterion is used to minimise the difference between predicted and actual data. We here not only map from parameters to data, but also from data to parameter values. Generally this step is not possible, even not unique, but in our special situation of zero-variate data, it is unique and we can study the bijection from data to parameter space and vice versa. This adds to our understanding of the role of scatter, where variations in environmental conditions, behaviour and measurement error induce scatter in data, and adaptation and selection induce scatter in parameter values.

The next section discusses the bijection, its assumptions and the boundaries of the data and parameter spaces. The focus is on conceptual aspects. The algorithms for the bijection in both directions are presented in Appendices B and C and details of the boundaries of the parameter and data spaces in Appendices D and E. These boundaries reveal an important role of a new statistic, called supply stress, which turns out to quantify the position of species in the supply–demand spectrum. This spectrum is worked out in Section 3, followed by a discussion of evolutionary constraints on parameter values in Section 4. The role of scatter in data and parameter values is discussed in Section 5. Finally a general discussion is meant to provide context for our findings, which are summarised in the conclusions section. All symbols are listed in Tables 1 and A2.

2. Bijection in nine dimensions

DEB theory is imbedded in general systems theory (Bertalanffy, 1968), where the state of the system (i.e. individual) is quantified by a set of state variables and the changes in state by a set of rule’s. The standard DEB model has reserve, structure and maturity as
basic state variables, but reproduction in adults needs a reproduction buffer as additional state variable and specific species-specific buffer handling rules, which also involves extra parameters. As mentioned before, Appendix A presents a quantitative summary. The ageing module involves two extra state variables: the amounts of damage inducing and damage compounds. Body temperature can be another state variable for endotherms and terrestrial ectotherms (Kearney et al., 2010); body temperature approximates local environmental temperature for most aquatic ectotherms. We here only consider situations of constant environmental conditions, see assumptions A1–A3 of Section 2.1, with the implication that all state variables can be written as functions of age. Since the model assumes weak homeostasis, i.e. the ratio of the amounts of reserve and structure remains constant during growth under constant environmental conditions, the ratio does not change after birth, and body weight becomes proportional to the amount of structure.

The parameters of the DEB model can be classified into core parameters, which affect changes in the state variables and auxiliary parameters, which concern the link between state variables (reserve, structure, maturity, etc.) and measured quantities (length, body weight, respiration, etc.). The standard DEB model (with the acceleration and the ageing modules) has 15 core parameters: \( \epsilon_f, \theta_f, \theta_{f0}, \theta_i, \delta, \tau, \gamma, \lambda_i, \lambda_f, \lambda_a, \lambda_h, \lambda_c, \lambda_d, h_a, s_c \). Tables 1 and A2 (of Appendix A) list all symbols and their units. Core parameters differ from compound ones, i.e. simple functions of core parameters, in that they relate to a single underlying process. So, core parameters have an intimate connection with mechanisms.

The number of required auxiliary (and core) parameters in any particular situation depends on the measurements that the model needs to predict, where the quest is for the minimum number. We do not consider those parameters here, meaning that we do not include digestion efficiency \( \kappa_f \) and maximum specific searching rate \( (v_f) \), which are two core parameters of the standard model. We do not deal with the chemical potentials of food and faeces. DEB theory has a module for isotope dynamics, which involves a number of reshuffling and fractionation parameters (Pecquerie et al., 2010). We do not consider those parameters here, but point to the problem that the complexity of the DEB model in terms of numbers of parameters depends on what the model needs to predict. If the model only needs to predict length as a function of time since birth at abundant food, the standard DEB model has only 3 (compound) parameters, since it reduces to the von Bertalanffy growth model (Pütter, 1920). We mention this to reveal the connection between number of required parameters and types of data that need to be predicted.

Table 1 lists the nine data points and parameters of the standard DEB model among which bijection exists under the assumptions of Section 2.1.

2.1. Assumptions

To define the mapping between data and parameter space, we need to make a number of assumptions.

A1 Temperature is constant and the reference temperature is \( T_{ref} = 293 \) K. If the actual temperature differs, \( a_b, a_p, a_n \) and \( R_m \) must first be temperature corrected. A typical Arrhenius temperature is \( T_A = 8 \) K, which can be used for this purpose in the absence of better information. The correction can be done by dividing the ages and multiplying the rate by temperature correction factor \( \exp(T_A/T - T_A/T_{ref}) \), see (Kooijman, 2010, Eq. (1.2)).

A2 Food is abundantly available. Feeding is not explicitly included here, meaning that we do not include digestion efficiency \( \kappa_f \) and maximum specific searching rate \( (v_f) \), which are two core parameters of the standard model.

A3 Surface-linked somatic maintenance \( (p_f) = 0 \). This primarily concerns investment into heating (for endotherms) and osmotic work (for freshwater organisms), which depends on environmental conditions. We thus assume that these conditions are such that our assumption holds.

A4 The chemical potentials of structure and reserve are \( \mu_j = 0.5 \) and \( \mu_s = 0.55 \) MJ C\(^{-1}\)mol\(^{-1}\), respectively. The bulk composition of dry biomass is a mixture of carbohydrates, proteins and fats (Kooijman, 2010, Table 4.2), which is species-specific, but the overall values are assumed to be insensitive to these variations. Chemical potentials of reserve and structure can be estimated from data on energy content of biomass at two (or more) food levels.

A5 Ratios of chemical elements in dry structure as well as dry reserve are C:H:O:N = 1:1.8:0:5:0.15. This fixes the molecular weight of reserve and structure to \( w_s = w_r = 23.9 \) g C\(^{-1}\). Notice that similarity of elemental frequencies does not imply similarity in chemical composition. Avoidance of this assumption, including the similarity between structure and reserve, requires measured elemental frequencies of biomass at two (or more) food levels.

A6 Only if the water content of reserve and structure are equal is the dry/wet weight ratio independent of nutritional conditions (as is the standard assumption in the ecological literature). We also make this assumption with the implication that the dry/wet weight ratio \( \delta_w \) has a simple relationship with specific density of biomass \( d_w \) and the specific density of structure \( d_s \), where the specific density of wet structure is \( d_{w}^s = 1 \) g cm\(^{-3}\) and the specific density of reserve equals that of structure. The water content of structure and reserve can

<table>
<thead>
<tr>
<th>Description</th>
<th>Symbol</th>
<th>Unit</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age at birth</td>
<td>( a_b )</td>
<td>d</td>
<td>Maturity at birth</td>
</tr>
<tr>
<td>Age at puberty</td>
<td>( a_p )</td>
<td>d</td>
<td>Maturity at metam.</td>
</tr>
<tr>
<td>Age at death</td>
<td>( a_n )</td>
<td>d</td>
<td>Maturity at puberty</td>
</tr>
<tr>
<td>Dry/wet weight ratio</td>
<td>( \delta_w )</td>
<td>–</td>
<td>Specific assimilation</td>
</tr>
<tr>
<td>Wet weight at birth</td>
<td>( W_b )</td>
<td>g</td>
<td>Energy conductance</td>
</tr>
<tr>
<td>Wet weight at metam.</td>
<td>( W_i )</td>
<td>g</td>
<td>Allocation fraction to soma</td>
</tr>
<tr>
<td>Wet weight at puberty</td>
<td>( W_p )</td>
<td>g</td>
<td>Spec. somatic maintenance</td>
</tr>
<tr>
<td>Ultimate wet weight</td>
<td>( W_w )</td>
<td>g</td>
<td>Specific cost for structure</td>
</tr>
<tr>
<td>Max. reproduction rate</td>
<td>( R_n )</td>
<td>#d(^{-1})</td>
<td>Ageing acceleration</td>
</tr>
</tbody>
</table>
be estimated from data on dry and wet weight trajectories during starvation.

A7 We refrain from the detailed specification of the handling rules for the reproduction buffer and only consider maximum reproduction rate as a mean over several reproduction cycles for a fully grown adult female. To avoid this assumption, we need reproduction data as a function of time. Buffer handling rules tend to be species-specific. Maximum weight as data point, see Table 1, is assumed to exclude the reproduction buffer.

A8 Reproduction efficiency $k_R = 0.95$, which stands for the fraction of reserve that is allocated to reproduction that ends up in offspring. In the case of reproduction by eggs this represents a conversion from reserve of the mother to that of eggs, so no chemical transformation is involved. This parameter can only be estimated if the full energy balance is available from data.

A9 Growth efficiency $k_G = 0.8$, which stands for the fraction of reserve that is allocated to growth (of structure) that ends up in structure. This involves a chemical transformation from reserve to structure. Growth efficiency can be estimated from e.g. growth data at two (or more) food levels. In cases where this parameter could be estimated, 0.8 turns out to be consistent with data.

A10 Maturity maintenance rate coefficient $k_I = 0.002$ d$^{-1}$, which stands for the maturity specific maintenance costs, if maturity is expressed in cumulative energy investment in maturaton. Maturity itself does not have mass or energy. The parameter can only be estimated from data if reproduction is measured at several food levels. In cases where this parameter could be estimated, 0.002 d$^{-1}$ turns out to be consistent with data.

A11 Gonapoz stress coefficient $s_G = 10^{-4}$, which quantifies how fast ageing accelerates during ontogeny. The parameter can be estimated from data on relative survival frequency as a function of age for endotherms it can be in the order of 0.1 (steeper decline of survival probability as a function of age). The value only affects survival by ageing and has no effect on the energy budget, but the energy budget affects ageing.

Assumptions A1–A3 relate to restrictions on environmental conditions under which data has been collected. Assumptions A4–A6 relate to body composition and assumptions A8–A11 species properties. All these assumptions can be avoided, but this requires more complex data, frequently at several food levels, and more advanced parameter identification methods (Lika et al., 2011). This list of assumptions leaves nine degrees of freedom for the dynamic energy budgets as specified by the standard DEB model with acceleration and ageing.

2.2. The algorithm of the bijection and its boundaries

The algorithm for the map from the 9-dimensional parameter space to the data space is presented in Appendix B and that from data space to parameter space in Appendix C. Both algorithms are coded in software package DEBTool (in Matlab) and this software shows that the bijection actually exists and its computation is fast.

The algorithm from data to parameters involves the solution of two implicit equations, each in one variable, step D8 and D15, where good initial values are available. This substantial reduction of computational complexity summarizes the significance of this algorithm. Given that the mapping between data and parameter space is a bijection, the map from parameters to data can be used to obtain the inverse mapping, by minimising the difference between predicted and observed data (down to zero in this case), which is typical in parameter estimation. This involves, however, a search in 9 dimensions, and requires high quality initial estimates and substantial computation. The present reduction to two times a search in one dimension and good initial estimates reduces the problem substantially. On top of that, the algorithm exposes the role of particular compound parameters that frequently pop-up in DEB theory, e.g. $g$, $k$, $k_M$, $L_m$, $L_p$, and shows why and how they can be obtained from data, when primary parameters cannot. Notice for instance that, thanks to DEB’s weak homeostasis assumption, scaled structural lengths can be obtained from weights in a simple way (see step D2 of Appendix C), but structural lengths themselves take quite a few more steps to obtain (step D12).

Not all combinations of parameter values and data values are allowed by the standard DEB model. The restrictions are specified in Appendices D and E, respectively. The most remarkable boundary is that for $k$ (BP6 of Appendix D), where $k$ must be between the positive roots of $k^2(1 - k) = S_g$ and the statistic $s_g = k_1 E_0/p_A$ is the supply stress. The name is inspired by the observation that this statistic quantifies the distance to the supply-end of the supply–demand spectrum, which will be discussed below. This boundary follows from the requirement that the maximum reproduction must be positive. We could also derive that $s_g < 2^3/3^2$ (BP5 of Appendix D), a constraint that follows naturally from the structure of the standard DEB model.

Fig. 1 shows that many vertebrates have a (relatively) large value for stress for juveniles. The metric $s_g$ is simpler than it seems, since $k_1 E_0/p_A$ represents the maturity maintenance rate of an adult and $s_G+1(p_A) = (p_A)$ the specific assimilation of an adult (which is after metamorphosis). Ultimate absolute assimilation is $p_M = [p_A/L_p]^3$ and ultimate absolute somatic maintenance is $p_M = [p_A/L_p]^3$. Supply stress can thus also be written as $s_g = p_A p_M / p_A$ evaluated under optimal environmental conditions (abundant food, thermo-neutral zone). Under constant food conditions the energy budget for juveniles and adults amounts to $p_J + p_C + p_A$, where $G$ stands for growth and $R$ for maturation or reproduction. The inequality sign is because growth is defined as the increase in structure, while reserve also increases, which has to be fuelled from assimilation. A fully grown adult does not grow any longer and reserve also does not increase: $p_C = 0$ and $p_A = p_M + p_R$. That the supply stress $s_g$ must be smaller than $4/27$ is clear from the observation that for a fully grown adult $p_M = p_A p_R$ and $p_J \leq (1 - \kappa) p_A$ as a consequence of the $\kappa$-rule. Substitution gives $s_g \leq (1 - \kappa) k^2$ for $0 < \kappa < 1$. Supply stress $s_g$ only depends on $\kappa$ via maximum structural length, which can be out-divided. Since somatic maintenance $p_M$ is proportional to volume and assimilation $p_A$ to surface area, $s_g = p_A [p_A]^2 f^3/s^3(p_A)$ shows that $s_g$ does not depend on the value of $\kappa$, but has a direct link with the possible range of $\kappa$, which moves down to zero at the maximum value of $s_g = 4/27$, where $\kappa = 2/3$. If $k_I = 0$, puberty can be reached for all food levels that support existence. The existence of a lower food level for reproduction demonstrates that $k_I > 0$ in practice (Lika and Kooijman, 2011).

The significance of simple explicit borders of the parameter space is that it allows for the use of genetic algorithms for finding the best fit. All parameter combinations that are outside the parameter space can be intercepted by a filter and a penalty returned to the estimation procedure. The filter should evaluate $s_g$ to compute $s_g$, which means that the algorithm for the map from parameters to data needs to be followed till step P9 and that scaled length at birth needs to be evaluated in step P5. The boundary at which maturation ceases at birth requires a numerical procedure that is discussed in Kooijman (2009b) and implemented in software package DEBTool.

Although the notion of the supply–demand spectrum is not new (Kooijman, 1993, p. 17), the next section further develops the concept and discusses quantitative aspects.
3. Supply–demand spectrum

The concept of (energy) budget itself already involves the notion for matching demand to supply of metabolites (Banavar et al., 2002), which applies to all species. Kooijman (2010) suggests that this matching is the main task of hormonal regulation at sub-organismal level. Beyond that, at the organismal-level, species can be ranked according to a supply–demand spectrum that roughly reflects where the controls of energetics are: from environmental to internal. The use of resources is ‘pre-programmed’ in demand-species and the individual tries hard to match this demand by eating enough. Supply-species hardly have such a program, or modify it in a flexible way, according to the possibilities offered by the environment. Table 2 compiles stylised eco-physiological properties of species that link to their position in the spectrum. No species are at the extremes of the spectrum.

Demand species have less metabolic flexibility to handle starvation in terms of shrinking and rejuvenation, but they compensate that by a higher talent for finding the last food item (=low half saturation constant), for which they need complex behaviour and good memory and sensors. The half saturation constant is in fact the ratio of the (specific) ingestion and searching rates, meaning that demand species have a large specific food searching rates. High peak metabolic activity, relative to the standard one, is part of the skills they need to capture (fast) prey and is connected to searching rate. Capillaries (in a closed circulatory system) make that an increase in heart beat is felt in all corners of the body (where muscles contract), which explains the link with a high peak metabolic rate. Only annelids, cephalopods and vertebrates have capillaries, all other animal species work with open circulatory systems, where an increase in heart beat has less consequences for tissues that are further away from the heart. Annelids probably have them to build up pressure when pushing their body through soil; without capillaries muscle contraction would transport fluid inside the body too easily and does not have the effect that the body is pushed forward. We see this as an adaptation to life in soils that has little to do with the evolution from supply to demand systems. Cephalopods and vertebrates have telolecithal eggs, which possibly relates to their closed circulatory system with which they mobilise yolk. The embryo being on the outside of yolk facilitates access to environmental oxygen and allows for high metabolic rates, compared to iso- or centro-lecithal eggs. Mammals have alecithal eggs, which probably relates to their foetal development.

Demand systems have (food) acquisition homeostasis, with thermal homeostasis as pinnacle. Many species (insects, reptiles) developed in the direction of thermal homeostasis via behaviour (sitting in sun or shade), some species (insects, tunas, sharks) sport metabolic heating (endothermy), but mammals and birds have fully mastered this art (after birth). Endothermy induces timing problems of ageing relative to maturation; food availability has seasonal controls and life cycles must fit seasonal cycles. If an endothermic mouse and an ectothermic lizard of the same body size and energy budget parameters would also have the same ageing parameters, the (warmer) mouse would live too short. Endotherms accelerate ageing (Gompertz stress coefficient $\kappa > 0$), starting with an extra-low ageing rate. This gives age-dependent survival probabilities that are high for a long time, and then suddenly drop. Survival curves of ectotherms drop much more gradually, as far as ageing is concerned (Kooijman, 2010, Chapter 6). Notice that many factors affect survival and ageing is rarely the most important one in field conditions. Birds and mammals also sport upregulation of metabolism before egg laying or during pregnancy and lactation: maximum feeding rate is temporarily increased (Kooijman, 2010). The rationale of this pattern is discussed below. Zoo keepers (and farmers) know that most birds can be stimulated to lay more eggs by removing freshly-laid eggs, which shows that egg production is not energy limited. Offspring production in birds is typically limited by parental care just before fledging, when food requirement is at maximum (Kooijman and Lika, 2014a).

Because supply stress $s_t$ relates assimilation (supply) to maintenance (demand) we suggest that it quantifies the distance to the supply-end in the classification of species in the supply–demand spectrum and consequently $s_t = 4/27 - s_d$ is the distance to the demand-end of the spectrum. The width of the supply–demand spectrum is thus $s_d = 4/27$ (Fig. 1). $\kappa$ is frequently very close to the upper boundary for zero reproduction, but not to the lower boundary. This is further discussed in Kooijman and Lika (2014a). Although maximum reproduction is around $\kappa = 0.45$ for supply-species (Kooijman and Lika, 2014a), $\kappa$ approaches 2/3 for demand-species.

<table>
<thead>
<tr>
<th>Supply</th>
<th>Demand</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eat what is available</td>
<td>Eat what is needed</td>
</tr>
<tr>
<td>Large half saturation coefficient</td>
<td>Small half saturation coefficient</td>
</tr>
<tr>
<td>Rather passive, simple behaviour</td>
<td>Rather active, complex behaviour</td>
</tr>
<tr>
<td>Sensors less developed</td>
<td>Sensors well developed</td>
</tr>
<tr>
<td>Can handle large range of intake</td>
<td>Can handle small range of intake</td>
</tr>
<tr>
<td>Low peak metabolic rate</td>
<td>High peak metabolic rate</td>
</tr>
<tr>
<td>Open circulatory system</td>
<td>Closed circulatory system</td>
</tr>
<tr>
<td>Iso- &amp; centro-lecithal eggs</td>
<td>A- &amp; telo-lecithal eggs</td>
</tr>
<tr>
<td>Typically ectothermic</td>
<td>Typically endothermic</td>
</tr>
<tr>
<td>Reserve density varies strongly</td>
<td>Reserve density varies little</td>
</tr>
<tr>
<td>Survives some shrinking well</td>
<td>Survives shrinking badly</td>
</tr>
<tr>
<td>Survives rejuvenation well</td>
<td>Survives rejuvenation poorly</td>
</tr>
<tr>
<td>Energetic birth control</td>
<td>Behavioural birth control</td>
</tr>
<tr>
<td>No upregulation for reproduction</td>
<td>Upregulation for reproduction</td>
</tr>
<tr>
<td>No acceleration of ageing</td>
<td>Acceleration of ageing</td>
</tr>
<tr>
<td>Evolutionary original</td>
<td>Evolved from supply systems</td>
</tr>
<tr>
<td>Has demand components</td>
<td>Has supply components</td>
</tr>
<tr>
<td>(maintenance)</td>
<td>(some food must be available)</td>
</tr>
</tbody>
</table>
This interpretation of $s_s$ is confirmed in Fig. 2, which presents it as a function of the minimum functional response, i.e., the food ingestion rate as a fraction of the maximum one of an individual of that size, that is required to reach puberty. It amounts to $f_{\text{min}} = \left(k_fE_{\text{f}}[\rho_{\text{M}}]^{2}/\kappa^{2}(1-\kappa)S_{M}^{3}[\rho_{\text{Am}}]^{1/3}\right)^{1/3} = (f^{3}s_{s}/\kappa^{2}(1-\kappa))^{1/3}$ and has a minimum for $\kappa = 2/3$ for non-accelerating species. The figure also shows that $s_{s}^{\text{max}}(f_{\text{min}}) = f_{\text{min}}^{3}/4$, which directly follows from the previous expression for $f = 1$ and $\kappa^{2}(1-\kappa) < s_{s} < 4/27$. The figure clearly shows that supply species can reach puberty for a much broader range of food intake levels, compared to demand species. Some mammals and birds have a minimum scaled functional response for reaching puberty close one. This explains why these taxa have upregulation of metabolism linked to reproduction. This upregulation is an extra module in DEB models, that is not part of the standard DEB model.

Fig. 3 shows that endotherms with low values for $f_{\text{min}}$ and $s_{s}$ have a high value for $\kappa$. The coupling between $\kappa$ and $s_{s}$ follows from the increase of the possible range of $\kappa$ with decreasing $s_{s}$. Yet it is remarkable that none of the endotherms in the add_my_pet collection have a low supply stress $s_{s}$ in combination with a low $\kappa$. These couplings require further investigation.

Another strong confirmation for the interpretation of $s_{s}$ comes from taxa that have a large value of $s_{s}$; these are exactly the taxa that can considered to be demand species on the basis of the criteria of Table 2: all invertebrates have a small supply stress $s_s$, but vertebrates have higher values. Fig. 4 is the same as Fig. 1 but now highlights the 5 classes of fish. While hagfish (Myxinidae) and ray-finned fish (Actinopterygii) are close to the supply end of the spectrum, cartilaginous fish (Chondrichthyes) tend to be closer to the demand end. One species of lobe-finned fish (Sarcopterygii), the coelacanth, turns out to be a supply species, while the Australian lungfish has demand tendencies. This strategy is probably open to lungfish, because they can switch off maintenance (torpor, although the non-Australian species can do this better). Lampreys (Cephalaspidomorphi) seem to have some demand tendencies, which possibly relates to their life style of ‘milking’ fish. Only the European brook lamprey is presently in the collection; more species are required for confirmation. Ray-finned fish (Actinopterygii) tolerate a very wide range of food levels (Kooijman, 2009a), which confirms their classification as supply species.

Birds and mammals are close to the demand end, where food intake is primarily controlled by metabolic needs, while most invertebrates are close to the supply end, where food intake is primarily controlled by food availability. Cnidarians are possibly the most extreme supply species with extreme capacity of shrinking and rejuvenation in response to starvation: some medusea can even rejuvenate till polyps (Piraino et al., 1996). Because cephalopods have a closed blood circulation system, telolecithal eggs, high peak metabolic rate, complex behaviour and superb vision, we expected to see tendencies for demand species in this taxon. Yet their $s_{s}$ values are small, which probably relates to their life style of suicide reproduction. They do not die by ageing and their size at death is considerably smaller than their asymptotic size, while most species approximate that size (insects being an exception, Kooijman, 2014). This means that their value for $s_{s}[\rho_{\text{Am}}]$ is relatively very large for species with that size at death, so $s_{s}$ is small; their range in body sizes at death is quite large.

Fig. 5 shows supply stress $s_s$ as a function of ultimate structural length of species. DEB theory has rules for the co-variation of parameter values (Kooijman, 1986), which are based on simple physico-chemical arguments. These rules imply that $s_{s}$ is expected to be independent of maximum body size, since $E_{\text{h}}$ increases with cubed maximum structural length, $[\rho_{\text{Am}}]$ with structural length, while $k_{f}$, $[\rho_{\text{M}}]$ and $s_{s}^{\text{max}}$ are independent of maximum structural length.
length. The figure supports this idea by illustrating that the evolution from supply to demand systems is possible for species of all maximum body sizes.

4. Evolutionary constraints on parameter values

DEB parameter values are individual-specific and are partly under genetic control, in the sense of quantitative genetics, while data, as presented in Table 1, has an intimate link with eco-physiological performance. Natural selection is on eco-physiological performance, so the relationship between parameters and data parallels that between genotype and phenotype. Let us consider a particular case study. Different species of ctenophores of similar ultimate body size lay eggs of different size that all hatch in a single day. This invites for the question of how this constraint on data translates into constraints on parameter values. Not all parameters contribute to age at birth $a_b = p_{M_2} a_2$, where $a_2$ given in step P6 of the map from parameters to data (see Appendix B). It turns out to be a function of $k_{M_2} = |p_{M_2} | / |E_{C_2} |$, $k = k_1 / k_{M_2}$, $g = v[E_{C_2} ] / k(p_{M_1} )$ and $v_{fl} = (k(1 - \kappa))E_{fl}/L_{M_2}$. Ultimate structural length is $L_\infty = S_M L_{M_1}$ with acceleration factor $S_M = l_j / l_1$ and maximum structural length is given by $L_{M_1} = k(p_{M_1} ) / |p_{M_1} |$. Scaled length at birth $l_1$ in s is also a function of $k$, $v_{fl}$ and $l_j$ and scaled length at metamorphosis $l_1$ involves $v_{fl} = (k(1 - \kappa))E_{fl}/E_{C_2} L_{M_2}$. Suppose that evolution does not affect $|E_{C_2} |$ and $k_j$ between related species, the constraints that $a_b < 1$ and $L_{M_1}$ is fixed must now be translated into constraints on $|p_{M_1} |$, $v_{fl}$, $|p_{M_{1}} |$, $E_{fl}$ and $E_{C_2}$. If we focus on the upper boundary $a_b = 1$, we can translate this into the problem of how these parameters can vary while $S_M v_{fl}/l_1 g$ remains fixed at value $L_{M_1} / \bar{a}_b$. We still need a numerical analysis to go to actual numbers, but the case beautifully illustrates the variety of evolutionary pathways that are open to achieve apicular eco-physiological performance. One possible route to increase size at birth, without affecting age at birth and ultimate length, is to increase $E_{fl}$ and $v$ (in a special way). Another one is to increase $\kappa$ via $g$ and compensate by changing $S_M$ and $v$. Yet another one is to increase $|p_{M_1} |$ and compensate by $S_M$; the route is via the maternal effect that reserve density at birth equals that of the mother at egg formation.

5. Role of scatter

Scatter is an unavoidable aspect of biological data. The relative contribution of measurement error is typically small, however. Most scatter relates to ‘biological variability’ which has genotypic and phenotypic aspects, especially if different types of data originate from different biological subjects and/or different research workers. The question about role of scatter is highly relevant, but also difficult to address. We here study the role of scatter in the form of sensitivity of the mapping using elasticity coefficients and present a numerical example. We explore the link between the elasticities on both directions.

The bijection $P$ from data $d = (d_1, \ldots, d_9)$ to parameters $p = (p_1, \ldots, p_9)$ has a differentiable inverse $D$, so it classifies as a $C^1$-diffeomorphism. In other words $P(D(p)) = p$ and $D(P(d)) = d$. A $9 \times 9$ matrix of elasticity coefficients $e_{ij}$ is associated to each point in the 9 dimensional parameter space and $e_{ij}$ to each point in the 9 dimensional data space.

Table 3 gives (9 dimensional) parameters and data that are connected by the bijection, including the relative error between $d$ and $P(D(p))$ and between $p$ and $P(D(p))$, respectively. The absolute relative errors vary from 0 till $1.8 \times 10^{-4}$. These errors reflect the accuracy of the numerical procedures that are used in the algorithm of the bijection, where numerical integration and root finding occurs. We randomly sampled the data and parameter space for mapping and noticed that the relative error could increase above 0.1 if $a_b < 0.5$ or $a_m > 10^4$ or $W_m > 1$ Mg. After filtering the random trials for these boundaries, the mapping in both directions had a typical relative error of 0.0005, but could occasionally increase till 0.05, while the errors in both directions correlated. These errors reflect accuracy settings in the numerical procedures in the mapping.

The product $e_{ij} e_{ij} = e_{ij} f_{ij} = I$ must hold. This can be proved as follows. Let $D = \text{diag}(d)$ and $P = \text{diag}(p)$. The elasticity matrices can now be written as $e_{ij} = D^{-1} \partial(P(d)) / \partial(p) \partial(p) / \partial(d)$ and $e_{ij} = P^{-1} \partial(a)/ \partial(d)$. The inverse function theorem (Apostol, 1974, p.372) learns that $(\partial(a)/ \partial(d))^{-1} = (\partial(d)/ \partial(a))^{-1} D$. As a result we have

$$e_{ij}^{-1} = D^{-1} \frac{\partial (\partial(d)/ \partial(a))^{-1}}{\partial(d)} = P^{-1} (\partial(a)/ \partial(d))^{-1} D = P^{-1} \frac{\partial (\partial(d)/ \partial(a))^{-1}}{\partial(d)} D = e_{ij}$$

Likewise we have $e_{ij}^{-1} = e_{ij}$ and $e_{ij} e_{ij} = e_{ij}$. The elasticities for the parameters, $e_{ij}^{-1}$, could not be obtained reliably by numerical differentiation; many values sensitively depend on the perturbation factor that was used, specially for small factors. The values in Table 3 were obtained from those for $e_{ij}$. The values for $e_{ij}^{-1}$ could only be obtained by plotting the numerical derivatives as a function of the perturbation factor and graphically back-extrapolate to perturbation zero. Many values were approximately linear in the perturbation factor; not a good sign, but still workable. The determinant of the matrix for the data elasticities was found to be $|e_{ij} f_{ij}| = 0.447$ in this numerical example.

The position of the zeros indicates the absence of information, so $\bar{a}_b$ has information for $\bar{a}_m$ but $\bar{a}_m$ has no information for $\bar{a}_b$. The reason is that, in the present simple implementation of the ageing module in the standard DEB model, energetics affects ageing, but ageing does not affect energetics. Since $|E_{C_2} |$ is proportional to $d_0$, the elasticity $(d_0/|E_{C_2} |) / d_0 = 1$, while none of the other parameters affect $d_0$. The most extreme elasticity is $(d_0/|E_{C_2} |) / a_0 a_2/|p_{M_1} | = -7.4$, that of $|p_{M_1} |$ for $a_0$ (lower panel of Table 3). The map from parameters to data is most sensitive to the parameter $k_1$, with the weights and maximum reproduction to be affected the most. The map from data to parameters is sensitive mainly to the ages at birth and puberty, $a_b$, and $a_m$, which affect all parameters except $\kappa$ and $|E_{C_2} |$ (small elasticities).

6. Discussion

Although application and testing of a theory or model are frequently combined in practice, their aims can be very different.
Elasticity coefficients of parameters for data, e.g. $p_A = 0.1$. The second last column gives the relative error of mapping forward, followed by backward. The data-elasticities were obtained by extrapolating the numerical derivatives to zero perturbation; the parameter-elasticities were computed from the data-elasticities.

We here study applicability of the standard DEB model and in particular the problem of parameter identification. The problem that we addressed is that some statistical aspects of parameter identification can be successfully studied with elasticity coefficients in the situation that a bijection exists between data and parameter values. In typical situations, where the number of data points (greatly) exceeds the number of parameters, identification depends on a large number of properties. Feeding and survival are intrinsically stochastic and this source of stochasticity can easily have rather complex implications for the statistical aspects of parameter estimation (Kooijman, 2009a). Many other sources of stochasticity also exist, such as variation of parameter values among individuals. With the bijection we can separate effects of stochasticity on parameter estimation from effects of the model structure and focus on the latter.

The structure of the standard DEB model is a mix of components with supply and demand organisation. Somatic maintenance is proportional to the amount of structure and maturity maintenance to the level of maturity, irrespective of the nutritional condition. So they have a demand-organisation. Allocation to growth and maturation or reproduction has a supply-organisation and fully depends on what is available. Shrinking and rejuvenation are required in the absence of resources, where the demand can no longer be satisfied (Augustine et al., 2011).

In our search for the boundaries of the parameter and data spaces, we identified a simple metric, called supply stress $s_s = p_A p_s / p_s$ for fully grown adults, which seems to quantify the distance to the supply-end in the supply–demand spectrum on which species can be ranked. We came to this particular interpretation by the direct link between $s_s$ and the range of functional responses that allow puberty to be reached and by the taxa that have a small demand stress. It is in itself already very remarkable that $s_s$, as estimated from parameters, does segregate taxa. The accuracy of parameter values is difficult to address but the existence of clear taxon-related patterns supports the idea that their values do reflect some eco-physiological properties. As far as we know, this is the first time that the supply–demand spectrum is formally recognised as a spectrum and quantified.

Table 2 lists a number of diagnostic properties of supply and demand species. Application of these ideas should reveal if these properties can be extended and/or refined. Parental care, for instance, is best developed in demand systems, but also well developed in e.g. particular groups of (social) insects. We presently work on the further extension of the add_my_pet collection with (holometabolic) insects, which will allow us to test if parental care matches patterns in supply stress. Parental care was previously identified as an alternative or supplementary strategy for metabolic acceleration (Kooijman, 2014) to ease the start up of feeding and digestion by the neonate, when experience is low and requirement of high quality food is high. Fig. 4 weakly suggests a link between acceleration and supply stress in ray-finned fish. Territorial defence might be connected to parental care since territorial defence is typically only shown during the breeding season. Storing food in deposits in preparation for bleak seasons, frequently combined with hibernation or torpor, might also be a trait connected to demand systems. A more systematic study on various taxa is required to link these traits to the position in the supply–demand spectrum.

Most animal research concerns species near the demand end of the spectrum, where food intake is not very sensitive to food availability. The result is that weight becomes age-dependent, which explains why many growth models in the literature are age-based. Size-based growth models do exist for demand species, e.g. Strathe et al. (2009), but are less frequent. Species at the supply-end of the spectrum show, however, that a huge weight variation is possible among individuals of the same age but experienced differences in

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food availability. Age-based growth models do not work for them, if differences in environmental conditions are involved. Research on ageing suffers from the same problem. Most research is again done on endotherms with a limited range of intake rates among individuals of the same body size. This restricts the effect of energetics on ageing, which, according to DEB theory, should be much bigger in supply species.

The evolution from supply to demand reflects an increase in homeostatic control: the capacity of individuals to run their metabolism independent from environmental conditions (temperature, food). It is obviously never perfect. DEB theory delineates five different types of homeostasis: (1) strong (metabolic pools have a constant chemical composition), (2) weak (ratios of pool sizes become constant during growth in constant environments), (3) structural (body shape does not change during growth), (4) acquisition (food intake less dependent on food availability), (5) thermal (body temperature independent from environment). The role of shape (structural homeostasis) concerns, in the context of DEB theory, the scaling of surface areas (transport) to volumes (mass conservation). It is remarkable that this role of shape comes back in the scaling of assimilation versus somatic maintenance in the metric $s$.

We studied all 21 organisational alternatives of models that have reserve and structure as state variables and comply to weak homeostasis and concluded that the $\kappa$-rule as implemented in the standard DEB model is the only possibility that is consistent with a number of stylised empirical facts on energetics (Lika and Kooijman, 2011). The most convincing empirical support for the $\kappa$-rule possibly comes from studies where $x$ changes with coherent consequences for growth, development and respiration (Mueller et al., 2012).

The $\kappa$-rule has profound effects on metabolic organisation and the distribution of its value over the species has surprises (Kooijman and Lika, 2014a, 2014b). The rule has the counter-intuitive implication that species can boost their growth and reproduction by wasting assimilates: the waste-to-hurry phenomenon (Kooijman, 2013). It now seems that the $\kappa$-rule also plays a deep role in supply–demand spectra and really shaped the evolution of metabolism.

7. Conclusions

• Given a number of assumptions on auxiliary parameters, a nine-dimensional bijection exists between core-parameter and data space. We present an efficient algorithm for this bijection, which can be used in the specification of initial values in parameter estimation methods for large data sets. The relationship between DEB parameters and data has similarities to that between genotype and phenotype.

• We found expressions for the boundaries of the data and the parameter space. These expressions can be used to filter parameter combinations in parameter estimation methods for large data sets.

• One of the boundaries involves a new metric, the supply stress, which turns out to quantify the location of species in the supply–demand spectrum. This spectrum reflects the internalisation of energetic control.

• We identified diagnostic properties of species for their position in the supply–demand spectrum and discuss the links between these properties.

• Invertebrates and ray-finned fish turn out to be close to the supply end of the spectrum, while other vertebrates have demand tendencies. We explain why demand species show up-regulation of metabolism in association with reproductive events and discuss evolutionary aspects.

• We discuss some properties of the bijection using elasticity coefficients. The most extreme elasticity coefficient is that of specific somatic maintenance for age at puberty; age at puberty strongly decreases for increasing specific somatic maintenance among species.

• We consider evolutionary constraints on parameter values and present alternative metabolic routes for changes in egg size under constraints on incubation time, as observed in ctenophores.

• The $\kappa$-rule for allocation of mobilised reserve to soma was found to be responsible for the supply–demand spectrum, in combination with surface area–volume relationships. The $\kappa$-rule was also found to be responsible for the waste-to-hurry phenomenon.

Acknowledgements

We like to thank all who contributed to the add_my_pet collection and Mike Kearney, Bob Kooi and Gonçalo Marques for helpful discussions. Jean-Christophe Poggiale contributed with the proof that the elasticity matrices for parameters and data are inverse to each other.

Appendix A. The standard DEB model with acceleration

Table A2 lists all symbols that are used in this paper, apart from the ones listed in Table 1. The notation follows the DEB rules; their rationale is explained in the DEB-notation document (see under references).

The standard DEB model has three state variables, energy in reserve $E$, structural length $L$ and maturity $E_M$. Maturity has no mass or energy and is quantified as cumulative (dissipating) energy investment. Development starts with age, structural length and maturity all zero, and an amount of reserve such that reserve density $E/L^3$ at birth equals that of the mother at egg formation (maternal effect). Foetal (and bud) development (mammals, several fish, salps, cnidarians) represents a variation on egg-development, where $p_A/[P_{Am}]^{a_2} = e^{ft}$, where $e$ is the scaled reserve density of the mother. The maternal effect rule determines the energy cost of an egg or foetus, apart from the reproduction efficiency $\kappa$, which quantifies the overhead costs for reproduction. Life stage switches are linked to maturity $E_M$ exceeding threshold values, which are fixed parameter values: birth $b$ (start of feeding and metabolic acceleration), metabolic metamorphosis $j$ (cessing of metabolic acceleration), puberty $p$ (cessing of matura-start of allocation to reproduction). The lengths at which these switches occur $(l_b, l_j, l_p)$ are not parameters, but depend on food history, i.e. food density $X(t)$ (so on scaled functional response $f(t)$). Temperature affects all rate parameters. The changes in the state variables are simple functions of the powers $p_{\alpha}$, which are given in Table A1: $(d/dt)E = p_{\alpha}E$, $(d/dt)L^3 = p_{C}[E_C]$, with $p = xp_{C} - p_{S}$ and $(d/dt)E_M = p_{R}$, with $p_{R} = (1 - \kappa)$. Maturation is ceased, and allocation to reproduction is started if $E_M = E_M^f$ (or $l \geq l_p$); this allocation involves the same power $p_R$. During acceleration in the early juvenile stage, maximum specific assimilation $[P_{Am}]$ and energy conductance $v$ increase with length; the scaling in Table A1 uses the values of $[P_{Am}]$ and $v$ at birth. No metabolic acceleration occurs if $E_M = E_M^f$ (i.e. $l = l_b$); metabolic metamorphosis might (e.g. in bivalves) or might not (e.g. in cephalopods) coincide with a morphological one. The ratio $l_j/l_p$ is the acceleration factor with which the values of $[P_{Am}]$ and $v$ at birth are multiplied to arrive at those after metamorphosis. The juvenile stage is absent if $E_M^f = E_M^f$ (i.e.
Table A1
The scaled powers \( p_A/[p_{am}]^{k_A} \), for \( \sigma = A.C.S.I. \), as specified by the standardised ont model with acceleration and without heating costs for an isomorph of scaled length \( I - L_{am} \), scaled reserve density \( \varepsilon = (E/\lambda)^{\frac{1}{2}}/[p_{am}] \) and scaled maturity density \( \mu = E_U/(E/C_{0})^{2} \) at scaled functional response \( f = K/(K + X) \), where \( X \) denotes the food density and \( K \) the half saturation constant. Maximum length \( L_{am} = k/[p_{am}] \), has only this interpretation in the absence of acceleration, where \( I_{am} = j \). Parameters: allocation fraction \( \kappa \), investment ratio \( g = (E/C)/(k/[p_{am}]) \), maintenance ratio \( k = 1/[E/C]/[p_{am}] \).

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<th>Late juvenile ( I_{j} &lt; l \leq I_{am} )</th>
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<td>Mobilisation, ( p_C )</td>
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<td>Mat. maint., ( p_l )</td>
<td>( e^{s} \times \frac{I_{am}}{I_{am}} )</td>
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\( I_p = I_{am} \); this occurs in e.g. *Oikopleura* and insects. The expression for the mobilisation power \( p_C \) follows from the weak homeostasis requirement: the chemical composition of the individual does not change during growth in constant environments (possibly after a short adaptation period). Feeding is proportional to structural surface area, so to squared length in isomorphs, i.e. individuals that do not change in shape during growth. Environmental conditions (temperature and osmotic value) are assumed to be such that surface-coupled maintenance costs (heating in endotherms, osmotic work in freshwater organisms) are negligible. The powers for ingestion and defecation occur in the environment, not in the individual, so they are excluded from Table A1. Food searching is not discussed here.

Survival as affected by ageing is modelled by assuming that the hazard rate of the individual is proportional to the density of damage compounds (modified proteins), which are continuously produced by damage-inducing compounds (modified DNA). The production of the latter is taken to be proportional to the rate at which reserve mobilised, since this reflects dioxyn consumption that is not associated to assimilation. Ageing is accelerated in some taxa (endotherms) by also increasing the density of damage-inducing compounds proportional to their concentration. The quantitative details and motivation are presented in Kooijman (2010, Chapter 6). The simplified expression for age at death that is used here assumes that life span is large relative to the growth period. In that case, the survival probability as affected by ageing reduces to

\[
Pr[a_m > t] = \exp \left( \left( \frac{\beta a_m}{h_C} - 1 \right) + \frac{t^2}{h_C} \right)
\]

with \( \beta a_m = \tilde{h}_a/\tilde{h}_C \) and \( h_C = s_C \gamma f^3/\tilde{h}_m \), see Kooijman (2010, Eq. (6.5)) The mean age at death, \( a_m \), equals the integral of this function over all positive times \( t \).

The nine parameters (with units) of the standard DEB model with acceleration are: specific maximum assimilation rate \( [p_{am}] \) (J d\(^{-1}\) cm\(^{-2}\)), energy conversion \( \nu \) (cm d\(^{-1}\)), specific somatic maintenance \( [p_{am}] \) (J d\(^{-1}\) cm\(^{-2}\)), maturity maintenance rate coefficient \( \kappa_l \) (d\(^{-1}\)), specific cost for structure \( [E_{C}] \) (dm\(^{3}\) d\(^{-1}\)), reproduction efficiency \( \kappa_R \) (-), maturity at birth \( E_0 \) (J), maturity at metamorphosis \( E_0 \) (J), and maturity at puberty \( E_0 \) (J).

The remaining four primary DEB parameters that are not discussed here are: specific searching rate \( [F_{am}] \) (dm\(^{3}\) d\(^{-1}\) cm\(^{-2}\)), digestion efficiency \( \kappa_D \) (-), ageing acceleration \( \tilde{h}_a \) (d\(^{-2}\)), and Gompertz stress coefficient \( \beta_G \) (-). A number of auxiliary parameters are required for various types of conversion: dry–wet weight, length–weight, mass–energy. They are shape coefficient \( \delta_{am} \) (-), specific density of wet structure \( \nu_0 \) (g cm\(^{-3}\)), chemical potential of reserve \( \mu_0 \) (J C\(^{-1}\)mol\(^{-1}\)), and chemical indices for hydrogen, oxygen and nitrogen of reserve and structure \( n_{H_2}, n_{O_2}, n_{N_2}, n_{H_2O}, n_{O_2}, n_{N_2} \) (-). These parameters depend on the type of measurement, not on the structure of the DEB model. The DEB model obtains respiration from the conservation law for chemical elements, which involves the chemical indices.

Appendix B. The algorithm for map from parameters to data

The algorithm has 18 steps and requires the computation of a number of compound parameters that play a role in DEB theory:

P1 maintenance ratio \( k = \tilde{l}/k_{LM} \), with somatic maintenance rate coefficient \( k_{LM} = [p_{am}] / [E_{C}] \); P2 dry/wet weight ratio \( \delta_W = dW/d_{w}^2 \), with specific density of structure \( dW = |k_{LM} / [E_{C}] / \nu_0 \); P3 energy investment ratio \( g = E_0 E_0 / (k_{LM}) \) and maximum structural length \( L_{am} = \kappa_{LM} / [p_{am}] / [E_{C}] \); P4 scaled maximum \( U_0 = E_0 / [p_{am}] \), \( \nu_0 = E_0 / (1 - \kappa) \) and \( \nu_0 = \nu_0 / \kappa \) with \( \nu = b_f, p \); P5 scaled length at birth \( \tilde{l} = \tilde{l} / [p_{am}] / [E_{C}] \), \( \nu_0 = \nu_0 / \kappa \); P6 scaled length at birth \( \tilde{l} = \tilde{l} / [p_{am}] / [E_{C}] \), \( \nu_0 = \nu_0 / \kappa \); P7 scaled exponential growth rate \( \rho_1 = g(1 - \rho - 1) / (1 - g) \) (between birth and metamorphosis); P8 scaled length at metamorphosis \( \tilde{l} = \tilde{l} + \rho_{am} (dW/d_{w}^2) \), with \( (dW/d_{w}^2) = \rho_1 / 3 / (1 - \rho - 1) / (1 - g)\); P9 scaled ultimate length \( \tilde{l}_m = \tilde{l}_m + \rho_{am} / [E_{C}] \); P10 scaled length at puberty \( \tilde{l} = \tilde{l} + \rho_{am} / [E_{C}] \), with \( (dW/d_{w}^2) = \tilde{l}_m / 3 / (1 - \rho - 1) / (1 - g)\); P11 scaled age at metamorphosis \( \tilde{l} = \tilde{l} + 3 \rho_{am} / (1 - \rho - 1) \); P12 scaled von Bertalanffy growth rate \( \rho_6 = (3 + 3)/ (1 - g) \); P13 scaled age at puberty \( \tilde{l} = \tilde{l} + \rho_{am} / (1 - \rho - 1) \); P14 ages \( \tilde{l}_m = \tilde{l}_m + \rho_{am} / (1 - \rho - 1) \); P15 structural lengths \( \tilde{l}_m = \tilde{l}_m \), with \( \tilde{l}_m = b_f, p \); P16 wet weights \( \tilde{W} = (dW/d_{w}^2) \); P17 maximum reproduction rate \( \tilde{R}_m = \tilde{R}_m / [E_{C}] / (1 - \kappa) \) with initial reserve \( E_0 = \tilde{E}_0 / [E_{C}] / (1 - \kappa) \) and initial scaled reserve \( \tilde{E}_0 = (3g / (3g_0) / \tilde{l} - \tilde{b}_0 / \tilde{b}_0) \); P18 age at death \( a_m = \tilde{r} / (6g / [E_{C}] / \tilde{h}_m \tilde{l}) \), where \( \tilde{r} \) is the gamma distribution.
The computation of scaled length at birth \( l_b \) in step P5 is by far the most demanding, but efficient routines based on Kooijman (2009b) are available in software package DEBTool. Numerical integrations are required in \( l_p \), \( p \) and \( T_a \) as well, which reduces accuracy. This algorithm has been coded in function iget_params_9 of DEBTool.

Appendix C. The algorithm for map from data to parameters

This algorithm has 16 steps:

D1 acceleration factor \( s_M = (W_f / W_b)^{1/3} \). For non-accelerating species: \( W_f = W_b \) and \( s_M = 1 \) and \( a_0 = a_0^* \);

D2 scaled length at birth \( l_b = l_b / L_m = s_M (W_b / W_\infty)^{1/3} \), scaled length at metamorphosis \( l_j = l_j / L_m = s_M (W_j / W_\infty)^{1/3} \) and scaled length at puberty \( l_p = l_p / L_m = s_M (W_p / W_\infty)^{1/3} \) can be obtained from wet weights. Although structural lengths themselves cannot be accessed yet, their ratios can. Ultimate structural length \( L_m = L_m s_M \) and maximum structural length \( L_\infty \) will be given below when using ultimate wet weight \( W_\infty \). Maximum structural length \( L_m \) will be treated as a compound parameter and the interpretation only applies to non-accelerating species; ultimate structural length \( L_\infty \) exceeds \( L_m \) for accelerating species at abundant food;

D3 age at metamorphosis \( a_j = (a_0 \log s_M + a_0 \log s_j) / (\log s_M + \log s) \) with \( s = (s_M - l_j) / (s_M - l_p)^{1/3} \) and \( s_j = 3 \log s_M / (a_0 - a_0^*) \) during acceleration between birth and metamorphosis and the von Bertalanffy growth rate \( r_B = (1 / (a_0 - a_j)) \log (s_M - l_j) / (s_M - l_p) \) after metamorphosis. Their links with DEB parameters at abundant food are: \( a_j = k_M (1/l_b - 1) / (1 + 1/g) \) and \( r_B = (k_M / 3) / (1 - 1/g) \), see Kooijman (2010, Eq. (2.24)). So \( r_B = r_j / (3/l_b - 3) \) and substitution gives the result:

D4 cost for structure \( [E_C] = \mu_C d_V / W_b K_C = 26 151 \delta_{wv} \) \( J \) \( \text{cm}^{-3} \), given the assumptions. This directly follows from the definition of growth efficiency \( \delta_{wv} = \mu_C d_V / W_b [E_C] \);

D5 von Bertalanffy growth rate \( r_B = (1 / (a_0 - a_j)) \log (1 - 1/l_b) / (1 - 1/l_p) \), which directly follows from the definition \( L(t) = L_\infty - (L_\infty - L_m) \exp(-r_B t) \);

D6 maximum reserve residence time \( t_m = L_m / S = 1 / k_M = a_0 / 3.7 l_b \), where scaled length at birth \( l_b \) is given above. This is based on \( d/dt L(t) = \nu / 3 \) and the approximation that this holds during the full incubation time, leading to \( L_b = v a_0 / 3 \), see Kooijman (2010, Eq. (2.47)). However, reserve becomes depleted during incubation of eggs, increasing incubation time by a mean factor of 1.226 among species that are present in the collection. This value for \( t_m \) is an approximation that will be replaced in step D9;

D7 specific somatic maintenance cost \( [p_M] = 3 [E_C] / (1 - 3 r_m t_m) \). This is based on the von Bertalanffy growth rate \( r_B = [p_M] / 3 / ([E_C] + [p_M] t_m) \) at abundant food (Kooijman, 2010, Eq. (2.24)) after metamorphosis. Since \( t_m \) is an approximation, this value for \( [p_M] \) is also approximate (see next step);

D8 somatic maintenance rate coefficient \( k_M = ([p_M] / [E_C]) \), from its definition, see Kooijman (2010, Section 2.5.1). This value for \( k_M \) can be used as an initial value for a numerical procedure to solve \( k_M \) from the exact value for \( a_0 = \tau_0 / k_M \), with \( \tau_0 \) given...
by Kooijman (2010, Eq. (2.38)). So $k_M$ must be solved from $k_M q_0 = 3 \frac{dx}{dt} \left(1 - \frac{x}{x^2} \right) (a_0 - B_0 - B_0^2(2, 0) + B_0^4(2, 0))$, where $B_0(a, b)$ is the incomplete beta function, $a_0 = 3xg_{b/2} / b_0$, $x_0 = g_1 / (a_1 - g_1)$, $g = \frac{r_B}{(k_M / 3 - r_B)}$ (see D9), while $r_B$ is given in D5, $a_1$ in D3, $b_0$, $b_1$ in D2 and $s_2$ in D1. With this correct value for $k_M$, we obtain $[p_{M}] = k_M [E_C]$ to replace the value obtained in step D7;

D9 energy investment ratio $g = \frac{r_B}{(k_M / 3 - r_B)}$. This is based on the von Bertalanffy growth rate $r_B = \frac{k_M}{3} / (1 + 1 / g)$, see Kooijman (2010, Eq. (2.24)) and its definition $g = [E_C] / [E_M]$, see Kooijman (2010, Eq. (2.21)). The value for $l_m = (g k_M)^{-1}$ that was obtained in step D6 can now be replaced;

D10 allocation fraction $\kappa = 1 - R_m m_{EF} s_{s_4} (1.75 + g) / k_M$, with $k_M = 0.95$ as default. This is based on the maximum reproduction rate $\dot{R}_M = (k_M / E_M)((1 - \kappa) / \kappa) \dot{M}_M [E_C] [E_M] s_{s_4} (1.75 + g) - k_M E_M$ (Kooijman, 2010, Eq. (2.58)), the costs per (offspring) for a numerical procedure to solve $\dot{E}_M = \frac{dE_M}{dt} / E_M$, repeating steps D11 till D15 till conversion; this is based on $W_\infty = d^c_0 1 d^c_0 1$, see Kooijman (2010, Eq. (3.2)). We now have access to $L_0 = l_0 L_0$, $l_i = l_i L_0$ and $L_0 = l_0 L_0$;

D13 energy conductance $v = L_0 / l_0$, which directly follows from $t_{EM} = L_0 / v $;

D14 specific assimilation rate $\{p_{Am}\} = v [E_M] / [M] / [k_M]$. This follows from the definition of reserve capacity $[E_M] = [p_{Am} / v]$, see Section 2.3.1, and from maximum structural length $l_m = \kappa [p_{Am} / [p_{M}]]$, see Kooijman (2010, Sec. 2.6);

D15 maturity level at birth $E_M^{t_0} = ((1 - \kappa) / \kappa) E_M^{t_0}$, metamorphosis $E_M^{t_1} = ((1 - \kappa) / \kappa) E_M^{t_1}$ and puberty $E_M^{t_2} = ((1 - \kappa) / \kappa) E_M^{t_2}$ are based on $k = k_1 / k_2 = 1$, where maturity density does not change, see Kooijman (2010, Eq. (2.32)). The exact values can be obtained by integrating the ode's for reserve $E$ and maturity $E_M$ over structural length $l$. For that purpose the initial reserve $E(0) / E_0$ is obtained by step D9 of the previous subsection, while $E_M(0) / E_0 = 0$. The value for $\kappa$ can be used as an initial value for a numerical procedure to solve $\kappa$ from the exact value for $R_m$, repeating steps D11 till D15 till conversion;

D16 ageing acceleration $\dot{h}_R = 4.27 a_0^2 h_0 d s_{s_4}$, for small Gompertz stress coefficient $s_{s_4} = 10^{-8}$. This is based on $a_0 = \Gamma (4 / 3) / h_M$, with $h_M = h_0 / \sqrt{v / \alpha}$ and $\Gamma (4 / 3) = 0.893$, see Kooijman (2010, Eq. (6.6)).

This algorithm has been coded in function get_pars_9 of DEBtool.

Appendix D. The boundaries of the parameter space

The following formal constraints on parameter values apply at constant food at scaled functional response $f$, with $0 < f \leq 1$.

BP1 All parameters, i.e. $[p_{Am}], v, \kappa, [E_C], E_M^{t_0}, E_M^{t_1}, E_M^{t_2}, \dot{h}_R$, must be positive. The specific costs for structure $[E_C] > v d \mu / d V / \dot{W}_F$ follow from $k_M < 1$. Constraint BP6 is more restrictive than constraint BP1 for $\kappa$, however.

BP2 Allocation fraction $\kappa$ must be smaller than 1.

BP3 The maturity levels must increase: $0 < E_M^{t_0} \leq E_M^{t_1} \leq E_M^{t_2}$.

BP4 Scaled length at birth $l_B$ cannot exceed 1. For given energy investment ratio $g$ and maintenance ratio $k$, scaled length at birth $l_B$ increases with scaled maturity at birth $v l_B$. The maximum value for $l_B$ equals 1 for $\kappa = 1$, so a maximum value for $v l_B$ exists. To find this value, we rewrite (Kooijman, 2010, Eq. (2.28)) as

$$\frac{d}{dt} v l_B = \frac{u_0^2 g + 1}{u_0^2 + 1} - k v l_B$$

and remove scaled time considering

$$\frac{d}{dt} = -\frac{1}{3 u_0^2} \frac{g}{g + 1} - \frac{d u_0}{d u_0} = v l_B = \frac{v}{u_0^2 + 1} - 1$$

For $v_0 = 1$ and $l_B = 1$, we have $x_0 = g / (1 + g)$ and $x_3 = 3xg_1 / x_0$. Moreover $u_0^2 = (3g / (a_0 - B_0 - B_0^2(4, 3)))^2$ and $u_0^2 = 1 / g$. This set of 2 one's should now be integrated for $u_0$ from $u_0^2$ till $u_0^2$, where $l(u_0^2) = e$ and $v_0 = u_0^2$ for very small $e$. We should test that $l(u_0^2) = l_B = 1$, since the numerical integration is not trivial in this case.

BP5 Supply stress $s_b = k_2[E_C] / [p_{Am}]^2 f^3 s_3^2 (p_{Am})^2 \leq \frac{\kappa^2}{\kappa^2}$. allocation fraction $\kappa$ cannot be between 0 and 1 (see BP1 and BP2).

BP6 Allocation fraction $\kappa$ must be between the two positive roots of $x^2 - (1 - \kappa) / \kappa = s$. If $\kappa$ is at one of the boundaries, maturity at puberty is only reached asymptotically, maximum reproduction $R_m = 0$. If $s_b = \frac{\kappa^2}{\kappa^2}$, the two positive roots coincide and we have $\kappa = \frac{\kappa}{\kappa}$.

BP7 The constraint $a_b < a_m$ (see BD1) translates to $\tilde{h}_R < \tilde{f} (g) / (k_M a_b)$. The detailed argument is a bit more complex because death by ageing is stochastic and not all individuals need to reach puberty.

These boundaries have been coded in function filter_pars_9 of DEBtool.

Appendix E. The boundaries of the data space

The following formal constraints on data values apply at constant food at scaled functional response $f$, with $0 < f \leq 1$.

BD1 All data, i.e. $d_V, a_M, a_p, a_m, W_0, W_p, W_m, R_m$, must be positive.

BD2 Ages must increase during the life-cycle: $0 < a_p \leq a_m < a_m$. Aedes weights must increase during the life-cycle: $0 < W_p \leq W_p \leq W_m$.

BD4 A solution for $k_M$ from D8 must exist, which translates into

$$a_b f B < \frac{\lim k_M l_1 / a_m l_1}{\int_0^{a_b} (1 - x^2) / (a_0 - B_0 / (4, 2)) + B_0 / (4, 2))}$$

BD5 Puberty can be reached if maximum reproduction $R_m = 0$. Allocation fraction $\kappa$ only has a solution if $p_{M}^2 = s_3^2 l_1^2 / (p_{M})^2$ and $p_{R}^2 = k_2 [E_C] / k_2 [E_M]$. The quantities $s_3, R_m, [p_{M}], k_1, l_1, l_m$ and $p_{M}^2$ are treated here as functions of data (see algorithm of the bijection) and $E_0 = u_0^2 [E_C] / [k_M]$. So for small $\kappa$ the condition reduces to

$$u_0^2 [E_C] / k_M < s_3^2 [p_{M}] / p_{M}^2$$

Step D10 of the map from data to parameters shows that $R_m [E_M] \left(1.75 + g \right) < k_M s_3^2 l_1$ follows naturally from the
approximative estimate for \( \kappa \), but is an approximative constraint only.

These boundaries have been coded in function filter_data_9 of DEBtool.

References


Web references

Information about the DEB research program and its results can be found at (http://www.bio.vu.nl/thb/deb/); the software package DEBtool that has been used at (http://www.bio.vu.nl/thb/deb/deblab/debtool/); the add_my_pet collection is presented at (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/Species.htm); and its manual at (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/add_my_pet.pdf). The DEB notation and its rules are presented at (http://www.bio.vu.nl/thb/deb/deblab/Kooj2010_n.pdf).