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An introduction to Dynamic Energy Budget (DEB) models with special emphasis on parameter estimation

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Abstract

Theories of dynamic energy budgets (DEB) link physiological processes of individual organisms, such as ingestion, assimilation, respiration, growth and reproduction, in a single framework. In this introduction, I summarise the most encompassing DEB theory developed so far [Kooijman, S.A.L.M., 2000. Dynamic Energy and Mass Budgets in Biological Systems. Cambridge Univ. Press, Cambridge.] and compare it with various alternative approaches. I further review applications of the DEB model to particular species and discuss what sort of data sets are needed and have been used to estimate the various model parameters. Finally, I argue that more comparative work, i.e. applying DEB models to a wide range of species, is needed, to see whether we can understand the variability in parameter values among species in terms of their ecology and phylogeny.

Keywords: Dynamic Energy Budgets; Metabolic theory of ecology; Scope for growth; *Mytilus edulis*

1. Introduction

A dynamic energy budget (DEB) model of an individual organism describes the rates at which the organism assimilates and utilises energy for maintenance, growth and reproduction, as a function of the state of the organism and of its environment (Nisbet et al., 2000; Kooijman, 2001).The state of the organism can be characterised by, for example, age, size and amount of reserves, and the environment by e.g. food density and temperature. Dynamic energy budget models of individual organisms can be used as the basic building blocks in model studies of the dynamics of structured populations (Metz and Diekmann, 1986). Practical applications of DEB models include the optimisation of pest control (Van Oijen et al., 1995), the development of optimal harvesting strategies, including the harvesting of microbial products such as penicillin, and the reduction of sludge production in sewage treatments (Ratsak, 2001).

One of the most encompassing theories of dynamic energy budgets is the DEB theory developed by Bas Kooijman in the 1980s (Kooijman, 1986a, 2000). This theory resulted in the so-called κ-rule DEB model, which assumes that the various energetic processes, such as assimilation rate and maintenance, are dependent either on surface area or on body volume. The model further assumes that the assimilated products first enter a reserve pool, from which they are allocated to maintenance, growth and reproduction. The κ-rule says that a fixed fraction κ is allocated to maintenance and growth and that the remaining

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fraction 1-κ is available for development and reproduction. Though the κ-rule model is based on just a few straightforward assumptions concerning energy acquisition, reserve dynamics, energy allocation and maintenance, it is generally considered to be complex. For example, Brown et al. (2004a) states that DEB models are complex, using many variables and functions. He claims that there is room for a complementary and even more general approach. This apparent complexity and intractability may have hampered widespread application and testing of DEB models.

Aim of the present paper is therefore twofold. First, it intends to provide an easily accessible introduction to the basics of the κ-rule DEB model. From this introduction it should become clear that the DEB model is as general and simple as possible, without losing the essentials of the energy budget of an individual organism. An even more general approach does not seem feasible. Second, the paper should be of help to the practically inclined biologist who aims to link empirical observations on the physiology and energetics of a particular species to a theoretical energy budget model. In the second half of the paper emphasis is therefore put on practical aspects of estimating DEB parameters, using observational and experimental data.

2. DEB theory

2.1. Introduction

Kooijman's DEB theory describes the individual organism in terms of two state variables: structural body, quantified as volume V, and reserves, quantified as energy density $[E]$. The latter variable gives the amount of reserves E per unit of the structural body volume V. The square brackets in the notation of energy density indicate that the variable is expressed per unit volume. Appendix A provides more information on the notation used in DEB theory. The structural body and the reserves both have a constant chemical composition. This assumption is called the assumption of strong homeostatis. The amount of reserves can change relative to the amount of structural body, for example as a result of variable food conditions. This implies that the chemical composition of the total body may change. It also implies that a general model of the dynamic energy budget of an individual must distinguish between structural body and reserves. Organisms are able to survive prolonged periods of starvation, during which they continuously have to allocate energy to maintenance. These energy needs cannot be immediately fulfilled from feeding, which is another argument in favour of taking reserves explicitly into account.

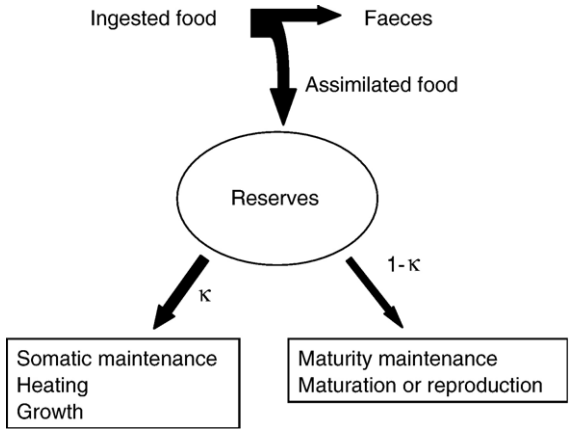

Fig. 1. Schematic representation of the κ-rule DEB model. Part of the ingestion is assimilated, the rest is lost as faeces. The assimilated products enter the reserve compartment. A fixed fraction κ of the flux from the reserves is spent on maintenance, heating (for endotherms) and growth (with a priority for maintenance), the rest goes to maturity (for embryos and juveniles) or reproduction (for adults) and maturity maintenance.

DEB theory assumes that assimilates derived from ingested food directly enter the reserves. A fixed fraction κ (read kappa) of the energy utilised from the reserves is spent on growth and somatic maintenance, the rest on development and reproduction. Based on this rule the DEB growth model has been called the κ-rule model (Fig. 1). Priority is always given to somatic maintenance, and if the energy utilisation rate from the reserves is no longer sufficient to pay for the somatic maintenance costs, the individual dies.

The energy ingestion rate $\dot{J}_X$ is proportional to the surface-area of the organism $V^{2/3}$ and is related to food density through a Hollings type II curve. Hence $\dot{J}_X = \{\dot{J}_{Xm}\} f V^{2/3}$, where $\{\dot{J}_{Xm}\}$ is the maximum ingestion rate per unit of surface area and f is the scaled functional response. The scaled functional response, which can vary between 0 and 1, is given by $f \equiv X/(X_K+X)$, where X is the food density in the environment and X_K the saturation coefficient. The saturation coefficient, or Michaelis-Menten constant, is the food density at which the ingestion rate is half the maximum. In terms of Hollings type II functional response it is equal to the reciprocal of the product of the area of discovery (or searching rate) and the handling time (Fig. 2). DEB theory assumes that the assimilation efficiency of food is independent of feeding rate. The assimilation rate (with dimension unit energy per unit time) can thus be written as $\dot{p}_A = \{\dot{p}_{Am}\} f V^{2/3}$, where $\{\dot{p}_{Am}\}$ is the maximum surface-area-specific assimilation rate. The precise

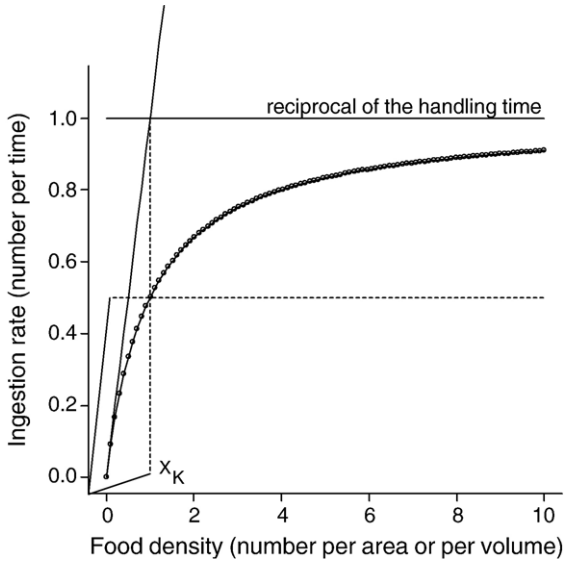

Fig. 2. The ingestion rate as a function of food density is described as a Holling's type II functional response, with the underlying idea that the animal is either searching for prey or handling prey. Searching occurs at a constant rate, and each prey requires a constant (expected) handling time. The initial slope of the function is given by the searching rate, whereas the asymptotic ingestion rate is given by the reciprocal of the handling time. The reciprocal of the product of the searching rate and the handling time is equivalent to the saturation coefficient X_K, which sets the prey density at which the ingestion rate is half the maximum rate.

value of $\{\dot{p}_{Am}\}$ will depend on the diet and the ratio $\{\dot{p}_{Am}\}/\{\dot{J}_{Xm}\}$ gives the conversion efficiency of ingested food into assimilated energy.

The assimilated products enter a reserve pool and it is assumed that the reserve density $[E]$ (energy reserves E per unit of body volume V) follows first order dynamics, which means that the rate at which the reserve density decreases (in the absence of assimilation) is proportional to the reserve density itself. Hence,

$$d[E]/dt = \dot{p}_A/V - c[E] = \{\dot{p}_{Am}\} f V^{-1/3} - c[E] \qquad (1)$$

where c is the proportionality coefficient that sets the rate at which the reserve density drops when no assimilation occurs. A maximum equilibrium reserve density $[E_m]$ occurs at maximum food density, and can be given (let $d[E]/dt=0$ and $f=1$) by $[E_m]=\{\dot{p}_{Am}\}V^{-1/3}/c$. Hence the coefficient c in Eq. (1) depends on volume, and Eq. (1) can be re-written as:

$$d[E]/dt = \{\dot{p}_{Am}\} V^{-1/3}(f - [E]/\{E_m\}) \qquad (2)$$

It follows that the equilibrium reserve density $[E]^*$ is proportional to the scaled functional response: $[E]^*=f[E_m]$. The assumption of first order dynamics of reserve density is one of the most important aspects of DEB theory. It is also the most difficult part of DEB, since the proposed mechanism underlying this assumption is rather complicated (Kooijman, 2000, pp. 246).

The utilisation rate $\dot{p}_C$ (with dimension energy per unit time), which is the rate at which energy is utilised from the reserves, can be written as the difference between the assimilation rate and the rate at which the reserves change $\dot{p}_C=\dot{p}_A-dE/dt$. According to the chain rule for differentiation, the rate of change of the reserves can be written as the rate of change of the structural volume multiplied by the energy density plus the rate of change of the reserve density multiplied by the structural volume: $\dot{p}_C=\dot{p}_A-dE/dt=\dot{p}_A-d(V[E])/dt=\dot{p}_A-[E]dV/dt-Vd[E]/dt$. Combined with Eq. (2), this gives

$$\dot{p}_C = \frac{\{\dot{p}_{Am}\}[E]V^{2/3}}{[E_m]} - [E]\frac{dV}{dt} \qquad (3)$$

When the energy density has reached equilibrium, the first term is exactly equivalent to the assimilation rate. The second term at the right-hand side is necessary to prevent dilution of the reserves due to growth.

A fixed proportion κ of utilised energy is spent on growth plus maintenance plus (for endotherms) heating, the rest goes to development (for embryos and juveniles) or to reproduction (for adults). Maintenance costs $\dot{p}_M=[\dot{p}_M]V$ are proportional to body volume (where $[\dot{p}_M]$ are the maintenance costs per unit of volume), and heating costs $\dot{p}_T=\{\dot{p}_T\}V^{2/3}$ are proportional to body surface area (where $\{\dot{p}_T\}$ are the heating costs per unit of surface area). Thus

$$\kappa\,\dot{p}_C = [E_G]dV/dt + [\dot{p}_M]V + \{\dot{p}_T\}V^{2/3} \qquad (4)$$

where $[E_G]$ are the energetic growth costs per unit of growth in structural body volume. Substituting Eq. (3) in Eq. (4) gives the growth equation

$$\frac{dV}{dt} = \frac{(\kappa\{\dot{p}_{Am}\}[E]/[E_m] - \{\dot{p}_T\})V^{2/3} - [\dot{p}_M]V}{\kappa[E] + [E_G]} \qquad (5)$$

Under constant food conditions the growth equation simplifies to

$$\frac{dV}{dt} = \frac{(\kappa f\{\dot{p}_{Am}\} - \{\dot{p}_T\})V^{2/3} - [\dot{p}_M]V}{\kappa f[E_M] + [E_G]} \qquad (6)$$

This equation is mathematically equivalent to the Von Bertalanffy growth model (Fig. 3). The ultimate volumetric length, which is the cubic root of the

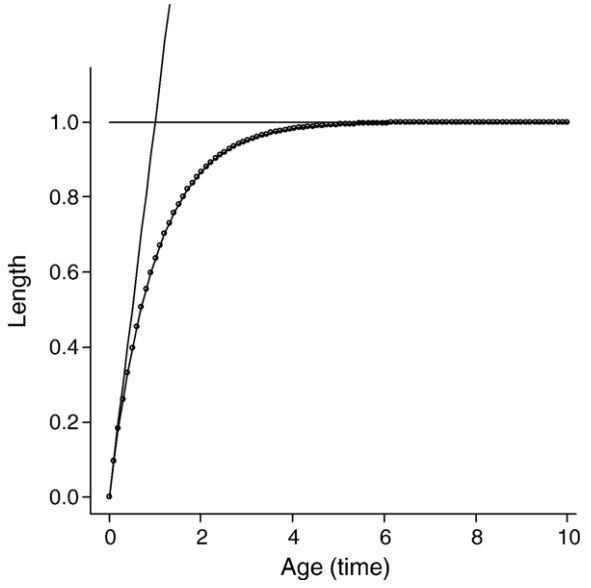

Fig. 3. Body length as a function of age. At constant food conditions, the DEB model predicts that volume growth follows the Von Bertalanffy growth equation, where the growth rate is given by the difference between a surface-area related term and a volume related term. Using the chain rule $dV/dt=(dV/dL)\cdot(dL/dt)=3(\delta_M L)^2\cdot dL/dt$ reveals the (non-autonomous first order) differential equation for the Von Bertalanffy length growth $dL/dt=\dot{r}_B(L_\infty-L)$. This equation can be solved to obtain length as a function of time (or age), i.e. $L(t)=L_\infty(1-\exp(\dot{r}_B t))$.

ultimate volume, equals $(\kappa f\{\dot{p}_{Am}\}-\{\dot{p}_T\})/[\dot{p}_M]$, and the Von Bertalanffy growth coefficient equals $\frac{1}{3}\frac{[\dot{p}_M]}{\kappa f[E_M]+[E_G]}$. The Von Bertalanffy growth model is, however, based on an entirely different biological rationale. DEB theory uses the energy conservation law and assumes that the difference between a supply (a fraction κ of the utilisation rate) and a demand term (the maintenance rate and the heating rate) is available for growth. Hence, the proximate control of growth is the utilisation rate, but the ultimate control is, of course, in resource intake by the individual from the environment (Fig. 1). In contrast, Von Bertalanffy did not apply the energy conservation law to the overall organism, but defined growth as the difference between anabolism (synthesis) and catabolism (breakdown).

By combining growth Eqs. (5) and (3), the utilisation rate can now be written as an explicit function of body volume and reserve density:

$$\dot{p}_C=\frac{[E]}{\kappa[E]+[E_G]}\times\left[\left(\frac{\{\dot{p}_{Am}\}[E_G]}{[E_m]}+\{\dot{p}_T\}\right)V^{2/3}+[\dot{p}_M]V\right] \quad (7)$$

Under constant food conditions (when the reserve density quickly reaches an equilibrium and becomes proportional to the scaled functional response: $[E]^*=f$ $[E_m]$), the utilisation rate is thus a function of surface-area and volume.

As was said above, a fixed proportion $1-\kappa$ of the utilised energy goes to development and reproduction. Embryos (which do not feed and do not reproduce) and juveniles (which feed but do not reproduce) use the available energy for developing reproductive organs and regulation systems. DEB theory assumes that the transitions from embryo to juvenile and from juvenile to adult occur at fixed sizes, V_b and V_p, respectively. The so-called κ-rule for allocation differs from other allocation rules in that no sudden change in the somatic growth pattern occurs at maturity. The rule also implies a similarity of growth patterns between the sexes. DEB theory further assumes that the reproductive organs require so-called maturity maintenance costs. Since the development stops at maturity (when the juvenile turns into an adult), these maturity maintenance costs do not increase any further after maturation. DEB theory states that for embryos and juveniles the ratio between the costs for development and the maturity maintenance costs is the same as the ratio between the costs for somatic growth and the (somatic) maintenance costs. Hence the utilisation rate allocated to development (first term at the right-hand side of Eq. (8)) and maturity maintenance (second term at the right-hand side of Eq. (8)) is for (ectothermic) embryos and juveniles given by:

$$(1-\kappa)\,\dot{p}_C=\frac{1-\kappa}{\kappa}[E_G]dV/dt+\frac{1-\kappa}{\kappa}[\dot{p}_M]V \quad (8)$$

The energy needed for maturity maintenance reaches its maximum at the size at maturity V_p. The size at maturity, i.e. the size at which a juvenile becomes an adult, is assumed to be constant. For adults, which no longer pay for development, the allocation to reproduction (first term at the right-hand side) and maturity maintenance (second term at the right-hand side) is given by:

$$(1-\kappa)\,\dot{p}_C=\dot{p}_R+\frac{1-\kappa}{\kappa}[\dot{p}_M]V_p \quad (9)$$

Combining Eqs. (7) and (9) will give an explicit expression for the reproduction rate (of ectotherms) $\dot{p}_R$. At constant food conditions and when the animal has reached maximum size, such expression simplifies to

$$\dot{p}_R=(1-\kappa)f\{\dot{p}_{Am}\}V_\infty^{2/3}-\frac{1-\kappa}{k}[\dot{p}_M]V_p \quad (10)$$

Table 1
The basic assumptions of the κ-rule DEB model

1. An organism is characterised by a structural body and a reserve density (i.e. amount of reserves per amount of structural body). The chemical composition of both structural body and reserves is constant, which is called the assumption of strong homeostasis.
2. Each organism starts its life as an embryo (which does not feed and does not reproduce). When the embryo has reached a certain degree of maturation, it changes into a juvenile (which feeds, but does not reproduce). Similarly, a juvenile changes into an adult (which feeds and reproduces) when it exceeds a given threshold value.
3. Ingestion is proportional to the surface area of the organism and depends upon food density by a Holling type II functional response. Recall that embryos do not feed.
4. A fixed fraction of the ingested food is assimilated and enters a storage pool, which is characterised by the reserve density.
5. The regulation of the reserve density follows a first-order process.
6. A fixed fraction κ of the utilisation rate goes to somatic maintenance, heating (for endotherms) and growth of the structural body (with a priority for maintenance), and the rest goes to maturity maintenance and (for embryos and juveniles) maturity or (for adults) reproduction.
7. Maintenance rate is proportional to structural volume and heating rate is proportional to the surface area of the organism.

An overview of the main DEB theory assumptions is provided in Table 1.

2.2. Temperature

The DEB theory uses the Van't Hoff-Arrhenius equation to describe the dependency of physiological rates on temperature. This equation has its origin in statistical thermodynamics, where the behaviour of a system containing a very large number of a single type of molecules is predicted from statistical considerations of the behaviour of individual molecules (Haynie, 2001). In its basic form the Van 't Hoff-Arrhenius equation looks like

$$\dot{k}(T) = \dot{k}_{\infty} \exp\left(\frac{-E_a}{kT}\right) \tag{11}$$

where $\dot{k}(T)$ is a reaction rate that depends upon the absolute temperature T (in Kelvin), $k$sub ∞ is a (theoretical) maximum reaction rate, which is the reaction rate when all molecules would react. The term $\exp(-E_a/(kT))$ is the Boltzmann factor, which gives the fraction of the molecules that obtain the critical activation energy E_a (in joules per molecule) to react. This fraction increases with increasing temperature. The constant k (not to be confused with the reaction rate $\dot{k}$) is the Boltzmann constant and equals 1.38 10^{-23} joule per degree Kelvin. The Van 't Hoff-Arrhenius equation can also be re-written in the form

$$\dot{k}(T) = \dot{k}_1 \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right) \tag{12}$$

where $\dot{k}_1$ is the reaction rate at a reference temperature T_1, and T_A the so-called Arrhenius temperature (which equals E_a/k).

Glasstone et al. (1941) showed that the Van't Hoff-Arrhenius equation is approximate for bimolecular reactions in the gas phase. Kooijman (1993, 2000) emphasises the enormous step from a single reaction between two types of particles in the gas phase to physiological rates where many compounds are involved and gas kinetics do not apply. He therefore regards the application of the Van't Hoff-Arrhenius relation to physiological rates as an approximation only, for which the parameters have to be determined empirically. For this reason, Kooijman prefers the use of an Arrhenius temperature instead of the use of an activation energy, which would give a false impression of mechanistic understanding. Similar to Kooijman, Clarke (2003, 2004) and Marquet et al. (2004) stress that the Van't Hoff-Arrhenius equation is just a statistical generalisation, and they too conclude that at present we still lack a clear understanding of the relationship between temperature and metabolism at the organismal scale.

2.3. Size and shape

The size of the structural body, quantified as volume V, is one of the two basic state variables of the DEB model. All energetic processes are directly related to V. Maintenance rate, for example, is proportional to volume V, whereas assimilation rate is proportional to the so-called volumetric surface area $V^{2/3}$. In practice structural volume is not easily measured. Measurements of length are usually much easier to obtain, and if an organism does not change in shape during growth, then each length measure can be used to predict volume by using a calibration curve of the form

$$V = (\delta_M L)^3 \tag{13}$$

where δ_M is a shape parameter, whose value, of course, very much depends upon the type of length measure L taken. For shells, for example, length may be measured

as height or width. Mammals may be measured including or excluding the tail, etc.

2.4. Compound parameters and a dimensionless representation of the DEB model

The differential equations for energy density (Eq. (2)) and structural volume (Eq. (5)) are the core of the DEB model. The dynamical behaviour of the system as defined by these coupled equations (i.e., reserve dynamics and growth) can be most easily understood by using the dimensionless form of the equations. Using the dimensionless variables scaled energy density $e=[E]/[E_m]$, scaled volumetric length $l=V^{1/3}/V_m^{1/3}$ (where, for ectotherms, maximum volumetric length $V_m^{1/3}$ equals $\kappa\{\dot{p}_{Am}\}/[\dot{p}_M]$) and scaled time $\tau=t[\dot{p}_M]/[E_G]$, Eqs. (2) and (5) turn into:

$$\frac{de}{d\tau}=g\frac{f-e}{l} \tag{14}$$

and

$$\frac{dl}{d\tau}=\frac{g}{3}\frac{e-l}{e+g} \tag{15}$$

where the compound parameter g is given by the ratio $[E_G]/(\kappa[E_m])$. Similarly, the dimensionless form of the utilisation rate (expressed as the scaled energy flux or power, i.e. $\dot{p}_C\frac{[E_G]}{[E_m]L_m^3[P_M]}$) is given by $\frac{eg}{e+g}(gl^2+l^3)$ and the dimensionless form of the assimilation rate by gfl^2.

Apparently, the dimensionless compound parameter g is the only parameter that truly affects the dynamics of the two equations system. This observation is in accordance with the suggestion of Fujiwara et al. (2005) that information on g in the data comes from the autocorrelation in the size trajectory. The parameter g has been given the name 'energy investment ratio' as it stands for the energetic costs of new structural volume $[E_G]$ relative to the maximum available energy for growth and maintenance $\kappa[E_m]$. The parameter 'maximum energy density' $[E_m]$, and the two compound parameters 'maximum volumetric length' $\kappa\{\dot{p}_{Am}\}/[\dot{p}_M]$ and 'maintenance rate coefficient' $\dot{k}_M=[\dot{p}_M]/[E_G]$ scale the two state variables and time to their dimensionless equivalents. The 'maintenance rate coefficient' stands for the ratio of the costs of maintenance to structural volume synthesis. Only four parameters are thus needed to fully characterise the dynamics of the reserves and the structural body. This implies that observations on assimilation rate, reserve dynamics (including utilisation rate) and growth alone do not suffice to enable estimation of all five (for ectotherms) basic DEB parameters $[E_G]$, $[E_m]$, $\{\dot{p}_{Am}\}$, $[\dot{p}_M]$, and κ (the list of basic parameters should actually also include the parameters V_b and V_p, which indicate the fixed sizes at which the transitions from embryo to juvenile and from juvenile to adult occur, but usually these sizes can be observed directly). The scaled reproduction rate (at constant food density and when the animal has reached its maximum size, see Eq. (10)) equals $(1-\kappa)g(f^3-V_p/V_m)$, and the appearance of the parameter κ implies that information on reproduction is also required for the estimation of all five basic DEB parameters.

The ratio of the area-specific assimilation rate to the maximum energy density occurs regularly in DEB theory (e.g. in Eqs. (3) and (5)) and has been called the energy conductance $\dot{v}=\{\dot{p}_{Am}\}/[E_m]$. The inverse of this compound parameter $\dot{v}$ can be interpreted as a resistance.

3. Alternative approaches

A dynamic description of the energy budget of an individual organism is a logical follow-up of a static description, which was the prevalent approach in the 1970s and 1980s. Various alternative dynamic models have been proposed, such as the net-production models (Lika and Nisbet, 2000) and the metabolic theory of ecology (Brown et al., 2004b). Below I will briefly discuss the static descriptions and the various dynamic alternatives.

3.1. IBP studies

Energy budget studies received an enormous impetus from the International Biological Program (IBP) that started in the 1960s. The flows of energy and matter into, within and out of an individual organism were divided into a number of separate fluxes. The most important ones distinguished are *ingestion* (total uptake of energy or mass), *defecation* (part of the ingestion that is not absorbed, but leaves the gut as faeces), *assimilation or absorption* A (part of the ingestion that crosses the gut wall, i.e. the difference between ingestion and defecation), *growth* dW/dt (part of the absorption that is incorporated in the body tissue of the organism), *reproduction* G (part of the absorption that is released as reproductive bodies), *excretion* E (part of the absorption that is released out of the body in the form of urine, or other exudates, with the exception of reproductive bodies), and finally *respiration* R (part of the absorption that is released in association with the

oxidation of organic compounds, and thus causes a net loss of CO_2). Assuming the conservation of energy and mass, the balance equation $dW/dt = A - (G + E + R)$ has played a key role in the IBP. Hitherto, many studies have followed this IBP recipe of constructing an energy budget for an individual animal. Since the budget must balance, a term particularly hard to measure was often found by difference. In the Scope for Growth (SFG) approach, for example, all terms apart from growth and reproduction are measured (Bayne and Newell, 1983). The SFG, which is the difference between absorption and excretion plus respiration, of a 'standard' animal (e.g. a blue mussel of 1 g dry mass) has been frequently used as an indicator of the 'health' of the ecosystem (Smaal and Widdows 1994; Widdows et al., 1995).

One of the major shortcomings of IBP-type energy budget studies is that the results are only descriptive and very hard to generalise, even towards animals of the same species but different in size. Measuring the SFG of a single individual of a particular size will not elucidate the link between the energy budget and, for example, the age-size relationship. Knowledge on the relations between all energy budget terms and body mass of the individual is required. The terms that were distinguished in the IBP approach have been chosen because they are relatively easy to measure, and not because their relationship to body mass could be easily derived from first principles. Respiration, for example, reflects the costs of many different processes. Apart from the basal maintenance costs of the body, which are, among other things, due to the maintenance of concentration gradients across membranes and the turnover of structural body proteins, it includes heating costs, costs that are directly coupled to the ingestion of food and costs coupled to the growth of body tissue. Whereas DEB assumes that all these costs depend in a different way on body size (e.g. maintenance costs relate to body structural volume, whereas heating costs relate to surface area), IBP-type studies usually apply allometric curve fitting to generalise the obtained findings to other size classes. A further complicating factor that is not accounted for in the IBP approach, is that not all surplus energy available for growth will immediately be used for growth of the structural part of the body. It may be stored temporarily in a reserve tissue buffer. As various processes, such as ingestion and maintenance, will basically be related to the structural part of the body, such distinction between a metabolically active structural part of the body and inactive reserve tissue seems to be a prerequisite for a proper understanding of energy budgets of individual organisms.

3.2. Net-production models

Various alternative dynamic energy budget models have been constructed (Nisbet et al., 1996, 2004; Lika and Nisbet, 2000) that have been classified as net-production models. These models differ from Kooijman's κ-rule model in that they first subtract the maintenance costs from the assimilated products, before they are allocated to other metabolic processes (growth, reproduction). Kooijman (2000, pp. 365) points to various theoretical problems with net-production models, one of them being that non-feeding animals (e.g. embryos or animals experiencing starvation periods) do have to pay maintenance costs anyway, which thus requires that extra switches have to be built in to pay maintenance costs from the reserves under such conditions. One might argue that theoretical arguments do not suffice, as models are always simplifications of the truth, and that the proof of the pudding is in the eating. A major challenge is then to find out what sort of experiments enable the selection of the most appropriate model (Noonburg et al., 1998).

3.3. Metabolic Theory of Ecology

The so-called metabolic theory of ecology (MTE) advocated by Brown and co-workers (West et al., 1997, 2001; Gillooly et al., 2002; Brown et al., 2004b) has received much attention over the last decade, despite a lack of generality of the proposed mechanism and a lack of internal consistency in the description of the energy budget of the individual organism (Van der Meer, 2006). Basis of the theory is the idea that whole-organism metabolic rate is limited by the internal delivery of resources to cells. Resources have to be distributed through branching networks, and it was suggested that the fractal-like designs of these networks cause the supply rate and hence the metabolic rate to scale as a 3/4 power of body volume. Such a closed branching network is, however, at best applicable to a minority of species. Apart for the vertebrates, closed networks do not exist in the animal kingdom. It was further assumed that the metabolic rate not only equals the supply rate, but also the maintenance rate, defined as the power needed to sustain the organism in all its activities. At the same time, the difference between supply and maintenance was assumed to be entirely used for the construction of new body tissue. Yet, you cannot have your cake and eat it, and, in fact, this ambiguity violates the first law of thermodynamics, as denoted by Makarieva et al. (2004). Another disadvantage of the MTE model is that it does not provide explicit

descriptions of some basic energy fluxes, e.g. the flux towards reproduction.

3.4. Species-specific models

All types of DEB models, whether it is the κ-rule DEB model or the net-production models, are relatively simple models aiming to have a wide applicability, throughout the animal kingdom and possibly beyond. This implies that species-specific aspects, such as, for example, the low feeding rate of larval nematodes, are not covered by these models. Practically inclined biologists therefore tend to develop their own species-specific models (Scholten and Smaal, 1998, 1999). A major problem with this approach is that such descriptions lack a common basis and usually contain many ad-hoc descriptions for the various sub-processes. So, apart from their complexity, this lack of a common basis hampers a comparison between these models. I believe that if species-specific aspects have to be taken into account, a 'phylogeny' of models is needed, where the κ-rule DEB model could play the role of the common ancestor and each progeny contains its own peculiarities. A good example is the work of Jager et al. (2005) on nematodes. They observed that nematodes differ from other animals in their initial growth being slower than expected on the basis of size alone, and were able to explain this lower growth by low feeding rates of the larvae. The size of the mouth cavity appeared to limit the feeding rate of the larval worms. Jager et al. (2005) incorporated this phenomenon into the κ-rule DEB model by correcting the ingestion rate using a size-dependent stress factor.

4. Parameter estimation and the link with empirical data: a short review of experimental approaches

So far, various studies have tried to estimate the five basic DEB parameters (the surface-area specific assimilation rate $\{\dot{p}_{Am}\}$, the volume-specific maintenance rate $[\dot{p}_M]$, the volume-specific costs of growth $[E_G]$, the maximum energy density $[E_m]$, and the fraction of the utilised energy spent on maintenance and growth κ), or, alternatively, the five compound parameters (the energy investment ratio g, the maintenance rate coefficient $\dot{k}_M$, the energy conductance $\dot{v}$, the maximum volumetric length L_m, and the Von Bertalanffy growth coefficient $\dot{r}_B$) for one or a few specific (metazoan) species. Examples are studies of daphnids *Daphnia magna* and *D. pulex* (Evers and Kooijman, 1989), pond snails *Lymnea stagnalis* (Zonneveld and Kooijman, 1989), blue mussels *Mytilus edulis* (Van Haren and Kooijman, 1993), the flatfish species dab *Limanda limanda*, plaice *Pleuronectes platessa*, sole *Solea solea* and flounder *Platichthys flesus* (Van der Veer et al., 2001), the nematode species *Caenorhabditis elegans*, *C. briggsae* and *Acrobeloides nanus* (Jager et al., 2005), and the delta smelt *Hypomesus transpacificus* (Fujiwara et al., 2005). These six studies used both observational (field) data and experimental data.

In the experiments both the initial state of the organism (age, size) and the state of the environment (food density, temperature) have been manipulated. Response variables include feeding rate, assimilation rate, respiration rate, growth rate and reproductive output. Most DEB parameters, such as the fraction of the utilised energy spent on growth and maintenance, the maintenance rate per unit of volume, and the maximum energy density, cannot be measured directly. One problem is that conceptual model processes do not have a simple one-to-one relationship to the measurable response variables. Respiration rate, as measured by oxygen consumption, for example, does not represent only maintenance costs, but also overhead costs of growth and reproduction. This implies that the estimation procedures are often quite complex. It appears that compound parameters, usually ratios of the primary parameters, are often more easily estimable.

Below, the experiments are categorised in seven classes, (*a*)–(*g*) (Table 2a, b). Each class will be shortly described.

4.1. Size and the functional response

Using the relationship between the ingestion rate $\dot{J}_X$ on the one hand and length L and food density X on the other hand

$$\dot{J}_X = \left\{\dot{J}_{Xm}\right\}(\delta_M L)^2 \frac{X}{X_K + X} + \varepsilon, \tag{16}$$

the surface-area-specific maximum ingestion rate $\{\dot{J}_{Xm}\}$ and the saturation coefficient X_K can be estimated. Note that the shape coefficient δ_M must be known beforehand. The relationship simplifies when either size or food density is kept constant. The assimilation efficiency is required to derive the assimilation rate from the ingestion rate. This efficiency is assumed to be constant and can be estimated by means of the Conover-ratio method (Conover, 1966).

For bivalves, the ingestion rate is usually estimated by determining the filtration rate and the food concentration in the filtrated water separately (Van

Table 2a
An overview of field data and experiments used for estimating DEB parameters

		a	b	c	d	e	f	g
Longitudinal				×	×		×	×
Treatment	None				×	(×)		×
	initial size	×	×			(×)		
	food density	×	×	×	i	∅	?	?
	temperature						×	
Response	intake rate	×						
	respiration rate		×		×	×		
	size/growth			×	×	×	×	×
	mass/growth				×	×		×
	cumulative reproduction			×				
	composition				×			
	survival time					×		

(a) Treatment factors and response variables in various types of experiments (coded a–g). When food density is not a treatment factor, food levels can either be kept at zero (indicated by the symbol ∅) i.e. in case of a starvation experiment, be ad libitum (∞), be a known initial amount that is depleted in the course of the observations (i), or be unknown (?).

Haren and Kooijman, 1993). Assuming that the filtration rate does not depend on food density, the surface-area specific filtration rate can be estimated by using

$$\dot{J}_W = \left\{\dot{J}_W\right\} V^{2/3} + \varepsilon, \tag{17}$$

where $\dot{J}_W$ is the filtration rate, $\{\dot{J}_W\}$ the surface-area specific filtration rate, and ε random observation error. Another feature of bivalve feeding is that it is often observed that the saturation coefficient is not constant, but depends on the silt content of the water (Pouvreau et al., 2006). This issue can be taken into account by more specific models of the feeding process, in which it is assumed that the food-acquisition apparatus can be temporarily clogged by silt particles (Kooijman, 2006).

4.2. Size and/or food density versus oxygen consumption rate

Van Haren and Kooijman (1993) used the oxygen consumption rate $\dot{J}_O$ as an approximation of the utilisation rate. Using Eq. (7)

$$\dot{p}C = \frac{[E]}{\kappa[E] + [E_G]}\left[\left(\frac{\dot{p}_{Am}[E_G]}{[E_m]} + \{\dot{p}_T\}\right) V^{2/3} + [\dot{p}_M] V\right],$$

which for ectotherms experiencing constant food conditions can be written as

$$\dot{p}_C = \frac{f[E_m][E_G]}{\kappa f[E_m] + [E_G]}\left(\frac{\{\dot{p}_{Am}\}}{[E_m]} V^{2/3} + \frac{[\dot{p}_M]}{[E_G]} V\right) \tag{18}$$

they arrived at $\dot{J}_O \propto (\dot{v}(\delta_M L)^2 + \dot{k}_m(\delta_M L)^3)$. Hence, by fitting the oxygen consumption rate as a linear function

Table 2b
An overview of field data and experiments used for estimating DEB parameters

	Short description	DEB parameters	References
a	Size and/or food density on ingestion rate (or filtration rate; or assimilation rate)	$\{\dot{J}_{Xm}\}$ or $\{\dot{J}_W\}$ or $\{\dot{p}_{Am}\}$, and X_K	E, H, V, Z
b	Food density and size on ingestion rate and respiration rate	$[\dot{p}_M]/\kappa$, $\nu/\dot{k}_M$, $g\{\dot{J}_{Xm}\}$	H
c1	Food density on growth curve	L_∞, $\dot{r}_B$; $\dot{k}_M$, $\dot{v}$ and g	F, H, J
c2	Food density on cumulative reproduction	κ, $\{\dot{p}_{Am}\}$, $[\dot{p}_M]$	J
d	Age of embryo within an egg on dry weight, reserve materials and respiration rate	$\dot{v}$, $\dot{k}_M$	Z
e1	Changes in respiration rate, body size and body mass during a starvation period	$\dot{v}$, $\dot{k}_M$, g/e_0	H
		$[\dot{p}_M]$, $[E_m]$	V
e2	Length on body size changes during starvation	$\dot{v}$ *or* $[\dot{p}_M]$	Z
e3	Initial size on survival time during starvation	$\dot{v}$, $\{\dot{p}_{A_m}\}/[\dot{p}_M]$ *or* $\dot{v}$, κ	Z
f	Temperature on growth rate	T_A	H, J
g	Observational length and mass (wet weight) data	δ_M, L_∞	H, V, Z

(b) The DEB parameters estimated using the experimental data from the experiment types a–g, and references. E refers to Evers and Kooijman (1989), F to Fujiwara et al. (2005), H to Van Haren and Kooijman (1993), J to Jager et al. (2005), V to Van der Veer et al. (2001), and Z refers to Zonneveld and Kooijman (1989).

(without a constant) of the volumetric surface area and the volume, they obtain (by taking the ratio of the two regression parameters) the ratio between the energy conductance $\dot{v}$ and the maintenance rate coefficient $\dot{k}_m$. Note that implicitly it is assumed that the part of the flux from the reserves that is not respired (and that is incorporated in either somatic tissue or in gonads) is negligible compared to the fraction that is actually respired.

If the food conditions are not constant, things get a bit more complicated. However, Van Haren and Kooijman (1993) used an experimental dataset in which ingestion rate instead of food density itself was measured. They subsequently used the relationship between utilisation rate on the one hand and ingestion rate and structural size on the other hand, which can be derived by inserting the equation for the ingestion rate $\dot{J}_X = \{\dot{J}_{Xm}\} f V^{2/3}$ into Eq. (18). This reveals

$$\dot{p}_C = \frac{\dot{J}_X [E_m][E_G]}{\dot{J}_X \kappa [E_m] + \{\dot{J}_{Xm}\} V^{2/3} [E_G]} \times \left(\frac{\{\dot{p}_{Am}\}}{[E_m]} V^{2/3} + \frac{[\dot{p}_M]}{[E_G]} V \right) \quad (19)$$

which can be re-written, using $\dot{J}_O = \eta \dot{p}_c$ (where η is a conversion coefficient that couples an oxygen flux to an energy flux) and $V^{1/3} = \delta_M \cdot L$, as

$$\dot{J}_O = \eta \frac{[\dot{p}_M]}{\kappa} \frac{\dot{J}_X}{\dot{J}_X / (\delta_M \cdot L)^2 + g\{\dot{J}_{Xm}\}} \times \left(\frac{\dot{v}}{\dot{k}_M} + \delta_M \cdot L \right) \quad (20)$$

Hence, the terms $\eta[\dot{p}_M]/\kappa$, $g\{\dot{J}_{Xm}\}$ and the ratio of the compound parameters $\dot{v}$ and $\dot{k}_M$ can be estimated.

It should be realised that if one is unwilling to assume that the part of the flux from the reserves that is not respired (and that is incorporated in either somatic tissue or in gonads) is negligible compared to the fraction that is actually respired, matters become more complicated.

4.3. Food density and growth and/or reproduction

If food conditions are more or less constant, growth curves can be used to estimate ultimate volume, which for ectotherms equals $\kappa f\{\dot{p}_{Am}\}/[\dot{p}_M]$, and the Von Bertalanffy growth coefficient, which equals $\frac{1}{3} \frac{[\dot{p}_M]}{\kappa f [E_M] + [E_G]}$. Note that both compound parameters contain the scaled food density f. It is not always appreciated that the Von Bertalanffy growth coefficient, often called the Von Bertalanffy growth rate, is not a growth rate, but represents the (negative) slope of the relation between the length growth rate and the length. In fact, DEB theory predicts that within the same species the Von Bertalanffy growth coefficient will increase with decreasing food levels (Fig. 4).

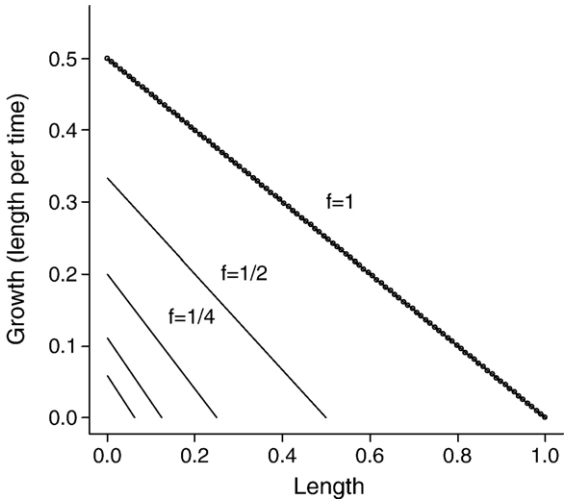

Fig. 4. Length growth rate as a function of body length for various food conditions (f). The Von Bertalanffy growth coefficient $\dot{r}_B$ is equivalent to the (negative) slope of the relation between the length growth rate and length $dL/dt = \dot{r}_B L_\infty - \dot{r}_B L$. The intercept $\dot{r}_B L_\infty$ is the initial length growth rate and is often indicated with symbol ω (Appeldoorn, 1982). DEB theory predicts that ultimate size is smaller at lower food conditions, but that the Von Bertalanffy growth coefficient increases with decreasing food conditions.

If food conditions are variable over the lifetime of an organism, it might be possible to estimate three parameters, e.g. $\dot{k}_M$, $\dot{v}$ and g, from the size trajectory. The size trajectory can be obtained by numerical integration of the two DEB differential equations (Fujiwara et al., 2005). The cumulative reproduction versus age can be obtained in the same way (both for constant and variable food densities). Recall that at constant food conditions and when the animal has reached maximum size, the reproduction rate (of ectotherms) is given by Eq. (10) (Fig. 5).

4.4. Growth and respiration rates of an embryo

Zonneveld and Kooijman (1989, 1993) used data on growth and oxygen consumption rates of embryos in eggs. The idea is that embryos do not feed, but that they use their high initial reserves for growth and maintenance. This phenomenon considerably simplifies reserve dynamics and reduces scatter related to variable

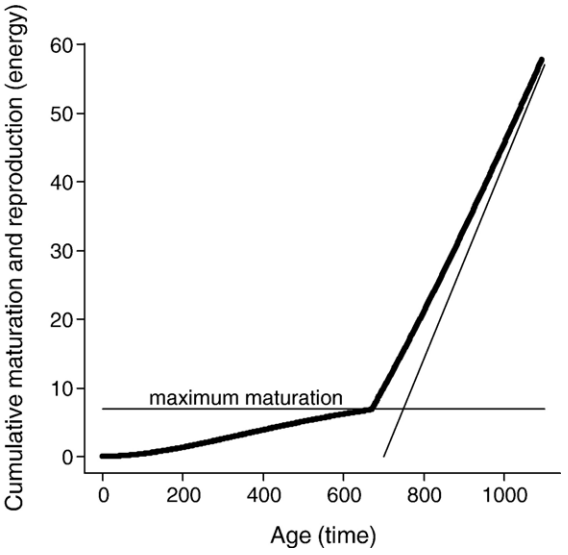

Fig. 5. Cumulative maturation and reproduction as a function of age. Scaled functional response is 1. At the age of maturity, i.e. when the structural body volume reaches V_P, the total investment in maturation has reached its maximum. From that moment onwards reproduction starts and the cumulative reproduction steadily approaches a diagonal asymptote, whose slope is given by Eq. (10) (see text).

food intake. For animals that do not feed (f=0) Eq. (2) simplifies to

$$\frac{d[E]}{dt} = -\frac{\{\dot{p}_{Am}\}}{[E_m]}[E]V^{-1/3} = -\dot{v}[E]V^{-1/3} \quad (21)$$

This simplified version of the differential equation for energy density and the differential equation for the structural volume (i.e. Eq. (5)) can be (numerically) solved in order to predict the growth of the embryo, and the decrease in reserve mass (which is proportional to $[E]V$) over time. Yolk mass was taken as equivalent to the reserves (Zonneveld and Kooijman, 1993), but for the pond snail reserves included glycogen, galactogen and proteins that are easily mobilised (Zonneveld and Kooijman, 1989).

4.5. Starvation experiments

For starving animals the rate of change in energy density is given by Eq. (21). If growth has also ceased, and structural volume V is constant, Eq. (21) can be easily solved:

$$[E] = [E]_0 \exp\left(-\dot{v}V^{-1/3}t\right) \quad (22)$$

The utilisation rate for animals that do not feed and do not grow simplifies to $\dot{p}_C = -Vd[E]/dt$, and the oxygen consumption rate (substituting Eqs. (21) and (22) and $\dot{J}_O = \eta\dot{p}_c$) can then be written as

$$\dot{J}_O = \eta\,\dot{v}[E]_0 V^{2/3} \exp\left(-\dot{v}V^{-1/3}t\right) \quad (23)$$

This approach, which has been followed by Evers and Kooijman (1989) and by Van Haren and Kooijman (1993) is not entirely consistent with the κ-rule, as it does not indicate for what purpose the difference between the energy flux to growth and maintenance (which according to the κ-rule should equal $\kappa\dot{p}_C = -\kappa Vd[E]/dt$) and the maintenance requirements, which equal $[\dot{p}_M]V$, is used.

4.6. Temperature and growth

DEB theory assumes that for a particular species, all rates (e.g. ingestion rate, respiration rate, growth rate) can be described, within a species-specific tolerance range, by an Arrhenius relationship using a single Arrhenius temperature. The rationale behind this assumption is that if different processes were governed by a different Arrhenius temperature, animals would face an almost impossible task of coordinating the various processes. Van Haren and Kooijman (1993) used the shell length growth rates of larval mussels at different food conditions and temperatures to estimate the Arrhenius temperature.

4.7. Size, mass and shape

The relationship between some length measure (e.g. shell length in the case of bivalves) and wet mass can be used to estimate the shape coefficient δ_M. However, special attention should be paid to the role of reserves and gonads. The idea is that the mass or volume measure should represent structural size, and should thus not be affected by the reserve density or the gonads. Hence dry mass or ash-free dry mass is certainly inappropriate. Wet mass can be used if reserves that have been used are replaced by water. The same should hold for gonads. If not, gonads may be dissected, but the physical removal of reserves will cause a problem, as they are partly stored in a variety of tissues. Specific density has to be estimated or known.

5. Estimation procedures and the blue mussel as an example

In this section, part of the parameter estimation procedure of Van Haren and Kooijman (1993) is repeated to illustrate the application of two statistical

approaches (simultaneous regression by means of weighted non-linear regression, and repeated measurements or time-series regression) not commonly applied in ecology, but very helpful in estimating DEB parameters. Data were read from the published graphs, which may have caused some inaccuracies in the estimates. Van der Veer et al. (2006) provide a more complete set of DEB parameter estimates for various bivalve species.

5.1. Simultaneous (non-linear) weighted least-squares regression

For the blue mussel *Mytilus edulis* Van Haren and Kooijman (1993) assumed a specific density of 1 g cm^{-2} in order to derive structural volume V from wet mass measurements and subsequently fitted the relationship $V=(\delta_M L)^3+\varepsilon$. They arrived at an estimate (±SE) of the cubic shape parameter δ_M^3 of $0.03692\pm7.59\cdot10^{-5}$, but did not indicate whether they used ordinary least squares (OLS) regression or weighted least squares (WLS) regression (Wetherill, 1986; see also Appendix B). From the graph (Fig. 6) it is clear that the error variance increases with increasing length. An OLS regression revealed an estimate of the shape parameter of $0.03683\pm6.39\cdot10^{-4}$, and a WLS (assuming that the error variance is proportional to cubic length) revealed an estimate of $0.03692\pm6.15\cdot10^{-4}$. The difference between these estimates is rather small.

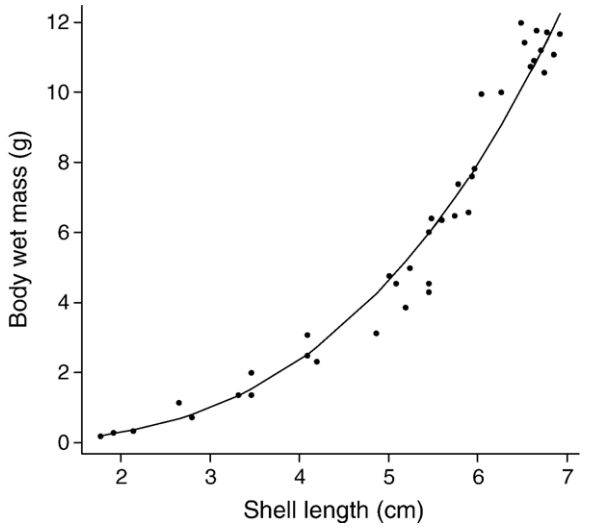

Fig. 6. The relation between body wet mass and shell length for the blue mussel *Mytilus edulis*. The fitted curve is based on a weighted least-squares procedure. The error variance clearly increases with length and the weights were chosen proportional to shell length. Figure after Van Haren and Kooijman (1993; Fig. 1).

Van Haren and Kooijman (1993) used experimental data from Winter (1973) to fit the function $\dot{J}_W=\{\dot{J}_W\}(\delta_M L)^2+\varepsilon$ between filtration rate $\dot{J}_W$ and shell length L. The parameter $\{\dot{J}_W\}$ is an area-specific filtration rate. The shape parameter δ_M was assumed to be known. Since filtration rates also depend upon food concentrations, the estimated value for $\{\dot{J}_W\}$ is only valid for the experimental food concentration, which equalled $40\cdot10^6$ cells dm^{-3}. Subsequently, they used other data from Schulte (1975) and Winter (1973) to fit filtration rate as a function of both food concentration and shell length. They used the function $\dot{J}_W=\{\dot{J}_{Wm}\}\frac{X_K}{X_K+X}(\delta_M L)^2+\varepsilon$, which follows from the assumption that the ingestion rate $\dot{J}_X$, which equals the filtration rate $\dot{J}_W$ times the food density X, follows Holling's type II functional response. The function contains two estimable parameters, the maximum area-specific filtration rate $\{\dot{J}_{Wm}\}$ and the saturation coefficient X_K. The parameter estimates from the second experiment can be used to predict an area-specific filtration rate for the first experiment. Applying a temperature correction (the first experiment was performed at 12 °C and the second experiment at 15 °C), using an Arrhenius temperature T_A of 7579 K, revealed an estimate for $\{\dot{J}_W\}$ of 0.499 $dm^3\ h^{-1}\ cm^{-2}$, on the basis of the data from the first experiment. Using the parameters of the second experiment, the obtained estimate for $\{\dot{J}_W\}$ is (slightly) different and equals 0.544 $dm^3\ h^{-1}\ cm^{-2}$.

However, if two or more functions contain common parameters it is perfectly possible to apply a single parameter estimation procedure. Suppose, for example, that two sets of data are available, and that for both sets a different (non-linear) equation has to be fitted, containing one or more common parameters. The error variance is not necessarily the same. Hence, a random variable Y is related to an independent variable X by a (non-linear) function $f(X,b)$ and a random variable Z is related to X by a (non-linear) function $g(X,b)$. The two functions contain a single common parameter b whose value has to be estimated, and the two types of observations have different variances, which are known up to a constant: $\mathrm{var}Y=w_Y\sigma^2$ and $\mathrm{var}Z=w_Z\sigma^2$. An estimate for the parameter b can then be obtained by a Weighted Least-Squares estimation (Appendix B)), that is by minimising

$$SS(b)=\sum_i\frac{(Y_i-f(X_i,b))^2}{w_Y}+\sum_j\frac{\left(Z_j-g\left(X_j,b\right)\right)^2}{w_Z}.$$

In practice these constants w_Y and w_Z are not known, but a commonly applied approach is to perform a two-step procedure. In the first step, the two equations are fitted separately, and the estimated residual variances are used

for determining the constants w_Y and w_Z. These constants are subsequently used in the second step, which is the (simultaneous) Weighted Least-Square estimation. Applying this procedure to the two above-mentioned data sets used by Van Haren and Kooijman (1993) resulted in an estimated maximum area-specific filtration rate $\{\dot{J}_{Wm}\}$ of 0.525 $dm^3\ h^{-1}\ cm^{-2}$ (Table 3).

Similarly, the data from Kruger (1960) on oxygen consumption rate versus shell length (Van Haren and Kooijman, 1993, their Fig. 8) and from Bayne et al. (1987, 1989) on oxygen consumption rate versus ingestion rate and shell length (Van Haren and Kooijman, 1993, their Fig. 9) could have been used simultaneously (Table 3, Fig. 7).

5.2. Longitudinal studies, repeated-measurements analysis and time-series regression

Quite often eco-physiological experiments are so-called longitudinal studies, which means that the response is not a single observation in time, but consists of multiple (or even continuous) observations in time. For example, respiration rate might be repeatedly measured over a prolonged period of growth or starvation. Similarly, treatment conditions may vary over time. Food density, for example, is usually kept at a constant level, but planned fluctuating food levels have been used as well. Field data often consist of longitudinal data, e.g. observed weight loss during periods of natural starvation.

Repeated-measurements studies, such as observations on the growth of individual organisms, have been analysed in two fundamentally different ways in the literature (Sandland and McGilchrist, 1979). The 'statistical' approach treats the repeated measurements on each individual as a multivariate observation or profile (Johnson and Wichern 1988) that can be analysed by a multivariate analysis of variance (MANOVA). Quite often, a further assumption is made on the dependence structure of the observations (i.e. so-called compound symmetry of the error covariance matrix is assumed, which means that all covariances are equal for each pair of years), which allows for the use of a univariate repeated measures analysis of variance (Winer, 1971; Potvin and Lechowicz, 1990). This 'statistical' approach thus allows for the dependence structure, but will leave a biologist, who requires an interpretation of the analysis of variance coefficients, unsatisfied. Alternatively, the 'biological' approach fits a biologically meaningful model, such as the DEB growth model, through the individual observations, and different parameters can be estimated for the different treatment

Table 3
Estimates of DEB parameters for the blue mussel, based on Van Haren and Kooijman (1993)

	Data	Original estimates	My estimates
1	Length and wet weight data	$\delta_M^3 = 0.03692 \pm 7.59 \cdot 10^{-5}$	$\delta_M^3 = 0.03692 \pm 6.15 \cdot 10^{-4}$ (using WLS with length as weights)
2	Size on filtration rate	$\{\dot{J}_W\} = 0.041 \pm 0.000675$ $dm^3\ h^{-1}\ cm^{-2}$	$\{\dot{J}_W\} = 0.378 \pm 0.00522\ dm^3\ h^{-1}\ cm^{-2}$ After temperature correction to 15 °C: $\{\dot{J}_W\} = 0.499\ dm^3\ h^{-1}\ cm^{-2}$
3	Food density and size on filtration rate	$\{\dot{J}_{Wm}\} = 0.83 \pm 0.098$ $dm^3\ h^{-1}\ cm^{-2}$ $X_K = 76\ 10^6 \pm 42\ 10^6$ cells dm^{-3}	$\{\dot{J}_{Wm}\} = 0.831 \pm 0.101\ dm^3\ h^{-1}\ cm^{-2}$ $X_K = 73.6\ 10^6 \pm 41.7\ 10^6$ cells dm^{-3}
2&3 combined			$\{\dot{J}_{Wm}\} = 0.831 \pm 0.0837\ dm^3\ h^{-1}\ cm^{-2}$ $X_K = 68.5\ 10^6 \pm 27.2\ 10^6$ cells dm^{-3} This gives: $\{\dot{J}_W\} = 0.525\ dm^3\ h^{-1}\ cm^{-2}$
4	Size on oxygen consumption rate	$\dot{v}/\dot{k}_M = 26.5 \pm 14.8$ mm	$\dot{v}/\dot{k}_M = 7.67 \pm 15.52$ mm
5	Size and ingestion rate on oxygen consumption rate	$\eta[\dot{p}_M]/\kappa = 0.056 \pm 0.025$ $cm^3\ O_2\ h^{-1}\ cm^{-3}$ $\dot{v}/\dot{k}_M = 5.3 \pm 6.5$ mm $g\{\dot{J}_{Xm}\} = 0.16 \pm 0.07$ mg POM $cm^{-2}\ h^{-1}$	$\eta[\dot{p}_M]/\kappa = 0.072 \pm 0.041\ cm^3\ O_2\ h^{-1}\ cm^{-3}$ $\dot{v}/\dot{k}_M = 0.27 \pm 0.54$ mm $g\{\dot{J}_{Xm}\} = 0.22 \pm 0.13$ mg POM $cm^{-2}\ h^{-1}$
4&5 combined			*Equal weighing of 4 and 5:* $\eta[\dot{p}_M]/\kappa = 0.0098 \pm 0.0148$ $cm^3\ O_2\ h^{-1}\ cm^{-3}$ $\dot{v}/\dot{k}_M = 6.69 \pm 10.71$ mm $g\{\dot{J}_{Xm}\} = 0.056 \pm 0.159$ mg POM $cm^{-2}\ h^{-1}$ *Non-equal weighing of 4 and 5:* $\eta[\dot{p}_M]/\kappa = 0.0511 \pm 0.0201\ cm^3\ O_2\ h^{-1}\ cm^{-3}$ $\dot{v}/\dot{k}_M = 0.672 \pm 0.543$ mm $g\{\dot{J}_{Xm}\} = 0.161 \pm 0.0664$ mg POM $cm^{-2}\ h^{-1}$

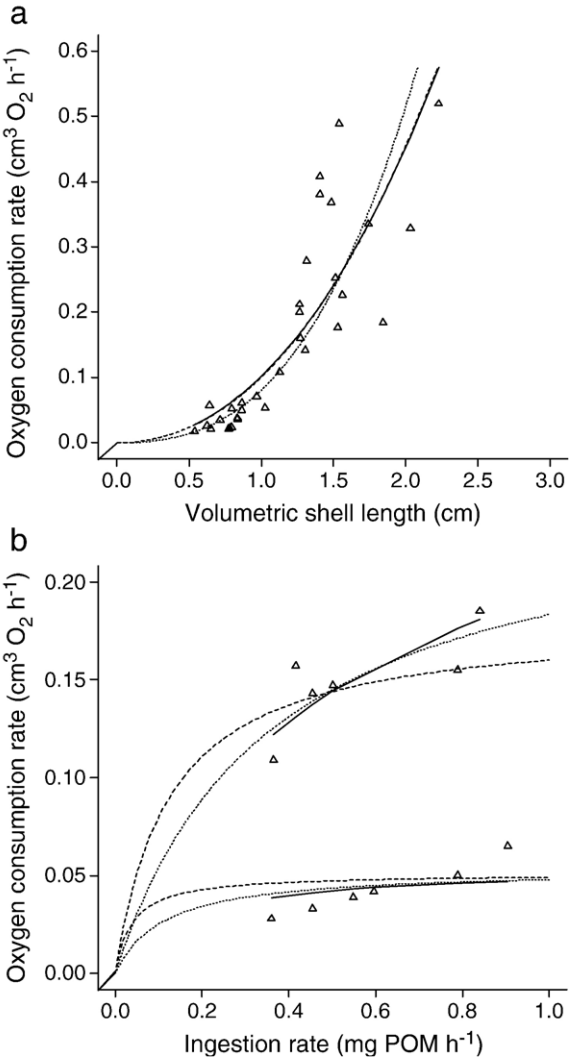

Fig. 7. Oxygen consumption rate as a function of (a) shell length and (b) ingestion rate and shell length for the blue mussel *Mytilus edulis*. In panel (b) squares indicate a shell length of 4.5 cm, circles a shell length of 2.5 cm. Curves are given by Eq. (20). Solid lines refer to the parameter estimates when the two datasets were used separately. Dotted and dashed lines refer to the jointly estimated parameters, using different weights. See also Table 3. Figure after Van Haren and Kooijman, (1993; Figs. 8 and 9).

levels. The data are related through time and the dependence structure in the underlying (growth) process can be explicitly taken into account by introducing a process-error term, or it can be ignored by treating all error as observation error (Priestley, 1981; Harvey, 1993; Hilborn and Mangel, 1997). If there is randomness in the underlying (growth) process, then error will propagate through time. Faster growth than expected during a certain time period will have its effect on length (and perhaps on growth) at later stages. Observation error, on the other hand, will not have any effects on length later on. The animal does not know what sort of observation errors we make. Excluding one type of noise in the analysis might lead to biases in parameter estimation (Hilborn, 1979; Quinn and Deriso, 1999). Recently, the so-called numerically integrated state-space method (NISS) has been advocated as being able to incorporate both types of error simultaneously (Kitigawa, 1987; De Valpine and Hastings, 2002). This method uses two models, one for the process including process error, the other for the observations, including observation error. Fujiwara et al. (2005) used this method to analyse the growth of the delta smelt under variable food conditions. They introduced process noise in terms of a, for each individual independently, randomly fluctuating food density, governed by a stochastic process with two unknown parameters. Here, Van Haren and Kooijman (1993) is followed and it is assumed that all error is observation error, which considerably simplifies analysis. For each set of parameter values the two differential equations of the DEB model are numerically integrated, and the model predictions concerning the size trajectory are compared to the observations by means of the residual sum of squares. A non-linear least-squares optimisation procedure (the Gauss-Newton method) is used to find that set of parameter values that minimise the sum of squares. It is impossible to estimate all DEB parameters on the basis of the size trajectory alone and even when most of the parameters were assumed to be known from other sources, the data were not appropriately fitted (Fig. 8).

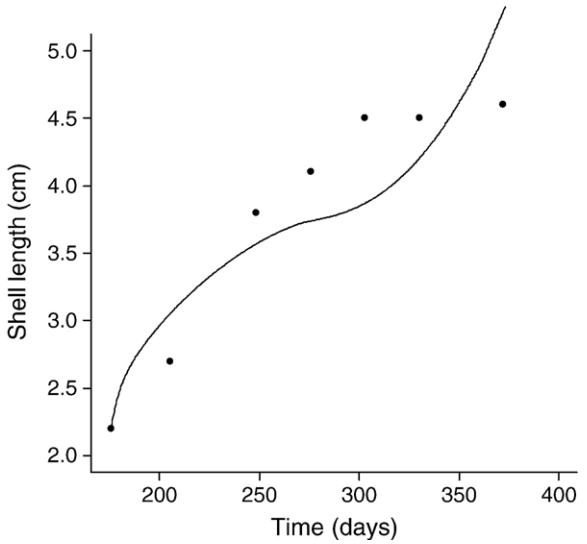

Fig. 8. Shell length of the blue mussel *Mytilus edulis* in the Oosterschelde estuary during 1985 and 1986. Figure after Van Haren and Kooijman (1993, Figs. 14 and 15).

Finally, it should be noted that in some cases, longitudinal studies are not repeated-measurements studies in statistical terms. If individual organisms are treated separately and measured only once, but at different points in time, then the observations are independent. Similarly, if only two observations are made in time (an initial observation and a final observation), then the difference between these two repeated measurements might be taken as the response variable (e.g. a growth measurement, instead of two repeated size measurements). This way, dependencies within an individual organism are implicitly taken into account.

6. Discussion

The six papers reviewed (Table 2b) showed a variety of approaches for estimating the DEB parameters. None of the papers has been able to obtain reliable estimates for all five basic parameters or, alternatively, for the set of compound parameters. Apparently, DEB parameters are not easy to estimate. A reason for this problem is that one of the two state variables, reserve density, is extremely hard to measure. The only reviewed paper in which reserve density was measured directly is Zonneveld and Kooijman (1989), but they considered the special case of embryo eggs, where the reserves are relatively easy to measure. Van der Veer et al. (2001) indirectly measured the maximum reserve density by assuming that flatfish reached their maximum reserve capacity at the start of a natural starvation period and lost all their reserves at the end of the period. An alternative approach was advocated by Van der Meer and Piersma (1994), who applied the idea of strong homeostasis to distinguish between reserves (what they called stores) and structural body. Strong homeostasis means that the chemical composition (for example, in terms of fat mass versus non-fat mass) of both structural body and reserves is constant, but not necessarily the same. For several bird species they analysed carcasses of a large number of individuals, including severely starved ones, in terms of fat versus non-fat mass. They observed that (after correcting for size) the relationship between lean mass and fat mass could be described by a two-piece (or broken) linear regression. The slope of one piece of the regression line represents the composition of the reserves, whereas the slope of the other piece reveals the composition of the structural body. Animals around that second piece had already started to break down their structural body. The breakpoint between the two pieces represents the structural body. Knowing the relation between size and structural body mass enables prediction of the actual reserves by subtracting the predicted structural body mass from the observed mass. The approach fails when reserves are replaced by water, as occurs in many aquatic animals.

If indeed observations on reserve density are lacking, it will be impossible to estimate all DEB parameters on the basis of information on food input, temperature and the size trajectory alone. Additional information on the various energy fluxes (such as assimilation, respiration and reproduction) is needed as well. From the re-analysis of the blue mussel data (Van Haren and Kooijman, 1993) it appears that severe estimation problems may occur when such data on energy fluxes are analysed in isolation. Even using the available data sets on oxygen consumption rate versus shell length and ingestion rate simultaneously, resulted in extremely large standard errors (Table 3, Fig. 7). Using a slightly different procedure of weighing the two data sets revealed completely different parameter estimates. Using as much information as possible in a single estimation procedure can reduce this problem of overfitting.

Writing the two DEB differential equations in a dimensionless form already yields some hints for a rule of thumb of how to estimate the basic DEB parameters. The dimensionless form only contained the parameter g, which is the energy investment ratio. Hence, this parameter might be estimated from the wiggles in the size trajectory, particularly when the scaled functional response varies over time in a known way (Fujiwara et al., 2005). Three other parameters, viz. maximum energy density and the two compound parameters maximum volumetric length and maintenance rate coefficient, are needed to scale the two state variables V and $[E]$ and the variable time t to their dimensionless equivalents. All five basic DEB parameters can be derived from estimates of these three parameters and of the parameters g and κ. The maximum energy density $[E_m]$ could be determined by providing animals with ad libitum food for a period long enough for the reserve density to reach the maximum reserve density. Subsequently, animals are starved for variable periods of time and the change in composition (e.g. in terms of fat, dry lean mass, and water) over time allows the estimation of both the structural body size and the maximum energy density (Van der Meer and Piersma, 1994). Maximum volumetric length $V_m^{1/3}$ and the maintenance rate coefficient $\dot{k}_M$ follow from the size trajectory of animals that have been able to grow up under ad libitum food conditions (if g is known, as the reciprocal of the Von Bertalanffy growth coefficient under ad libitum food conditions equals $3/(g\dot{k}_M)+3/\dot{k}_M$). The parameter κ follows from the reproduction rate of animals that

have reached (at constant and known scaled functional response) their maximum size, see Eq. (10). Hence, in principle no information on assimilation rates and respiration rates is needed to arrive at estimates of the basic DEB parameters. Although the measurements of these rates can be problematic (Van der Meer et al., 2005) and although the use of respiration rate as an approximation of the utilisation rate is not entirely correct, additional information on these rates may lead to more accurate parameter estimates. Hence, apart from knowledge on (long-term) growth trajectories and cumulative reproduction obtained under controlled (or at least known) conditions, an additional short-term experiment, in which both food conditions (using both constant and time-varying food conditions, ranging from zero to ad libitum) and temperature are varied in a systematic way, and in which assimilation, respiration, reproduction, size and body composition are measured at regular intervals, would contribute much in revealing reliable estimates of the basic DEB parameters.

Knowledge of the basic DEB (compound) parameters over a wide range of species opens opportunities towards a more quantitative understanding of the broad patterns in physiological diversity, for example in terms of phylogenetic relatedness and ecology (Spicer and Gaston, 1999).

Appendix A. A list of important DEB parameters

DEB uses a notation that is helpful in a quick interpretation of the equations. All rates have dots, which indicate that they contain the dimension 'per time'. All variables that are expressed per unit volume are given between square brackets. All variables that are expressed per unit surface area are given between braces. Notation from Kooijman (2000) is used. The earlier papers and books (Kooijman, 1986a,b, 1993) used slightly different notations, shown in the column Previous symbols.

Symbol	Dimension	Interpretation	Previous symbols
$[E]$	eL^{-3}	Energy density	
L	L	Body length	
V	L^3	Structural body volume	
F	–	Scaled functional response	
T	T	Temperature	
X	$\#l^{-2}$ or $\#l^{-3}$	Food density in the environment	
$[E_G]$	eL^{-3}	Volume-specific costs of growth	η, $[G]$
$[E_m]$	eL^{-3}	Maximum energy density	$[S_m]$, $[E_m]$
$\{\dot{J}_{Xm}\}$	$\#L^{-2}t^{-1}$	Surface-area-specific maximum ingestion rate	$\lfloor \dot{I}_m \rfloor$, $\{\dot{I}_m\}$
$\{\dot{p}_{Am}\}$	$eL^{-2}t^{-1}$	Surface-area-specific maximum assimilation rate	$\lfloor \dot{A}_m \rfloor$, $\{\dot{A}_m\}$
$[\dot{p}_M]$	$eL^{-2}t^{-1}$	Volume-specific maintenance rate	$\dot{\varsigma}$, $[\dot{M}]$
$\{\dot{p}_T\}$	$eL^{-2}t^{-1}$	Surface-area-specific heating rate	
T_A	T	Arrhenius temperature	
X_K	$\#l^{-2}$ or $\#l^{-3}$	Saturation coefficient	K
δ_M	–	Shape (morph) coefficient	
κ	–	Fraction of utilisation rate spent on maintenance plus growth	
g	–	Energy investment ratio $\frac{[E_G]}{\kappa[E_m]}$	
k_M	t^{-1}	Maintenance rate coefficient $\frac{[\dot{p}_M]}{E_G}$	$\dot{m}$
$\dot{v}$	Lt^{-1}	Energy conductance $\frac{\{\dot{p}_{Am}\}}{E_M}$	
L_m	L	Maximum volumetric length $\frac{\kappa\{\dot{p}_{Am}\}-\{\dot{p}_T\}}{[\dot{p}_M]}$	
L_∞	L	Ultimate volumetric length $\frac{\kappa f\{\dot{p}_{Am}\}-\{\dot{p}_T\}}{[\dot{p}_M]}$	
r_B	t^{-1}	Von Bertalanffy growth coefficient $\frac{1}{3}\frac{[\dot{p}_M]}{\kappa f[E_M]+[E_G]}$	

Appendix B. Weighted non-linear regression

B.1. Ordinary Least-Squares Regression

In Ordinary Least-Squares regression (OLS) the parameters of a linear regression model are estimated by minimising the sum of squares. In case of, for example, the regression-through-the-origin model $Y_i = bX_i + \varepsilon_i$, the problem is to find $\hat{b}$ that minimises the sum-of-squares function $SS(b) = \sum_i (Y_i - bX_i)^2$.

The solution to this problem is obtained by setting the derivative of the sum-of-squares function to b equal to zero. This reveals the so-called normal equation:

$$\frac{\partial SS(b)}{\partial b} = -2\sum_i X_i\left(Y_i - \hat{b}X_i\right) = \sum_i X_iY_i - \hat{b}\sum_i X_i^2 = 0 \text{ , resulting in } \hat{b} = \frac{\sum XY}{\sum X^2}.$$

The minimum sum of squares divided by $n-m$, where n is the number of observations and m the number of parameters (i.e. $m=1$ in the present case), provides an unbiased estimate $\hat{\sigma}^3$ of the variance of the observations. The variance of a linear function of independent random variables is given by $\mathrm{var}(uY_1+vY_2)=u^2$ var Y_1+v^2 var Y_2. Using this equality, it follows that

$$\mathrm{var}\hat{b} = \frac{\sum X^2 \mathrm{var}Y}{\left(\sum X^2\right)^2} = \frac{\sigma^2}{\sum X^2}.$$

B.2. Weighted Least-Squares Regression

The rationale for using Weighted Least-Squares regression (WLS) is usually the fact that the observations do have different variances, which are known up to a constant: $\mathrm{var}Y_i = w_i\sigma^2$. The parameters of, for example, the regression-through-the-origin equation $Y_i = bX_i$ can then be obtained by minimising

$$SS(b) = \sum_i \frac{(Y_i - bX_i)^2}{w_i}.$$

For convenience, the problem can be re-stated in terms of an OLS problem, by dividing both sides of the regression equation by $\sqrt{w_i}$. This gives a regression model with $Y_i' = Y_i/\sqrt{w_i}$ as the dependent variable, and $X_i' = X_i/\sqrt{w_i}$ as the independent variable. The OLS procedure then minimises

$$SS(b) = \sum_i (Y_i' - bX_i')^2 = \sum_i \left(\frac{Y_i}{\sqrt{w_i}} - b\frac{X_i}{\sqrt{w_i}}\right)^2 = \sum_i \frac{(Y_i - bX_i)^2}{w_i},$$

and is thus equivalent to WLS.

B.3. Non-linear Least-Squares Regression

The problem with non-linear equations is that the normal equations cannot be solved analytically. For example, in case of the model $Y_i = aX_i^b + \varepsilon_i$, the normal equations are given by

$$\frac{\partial SS(a,b)}{\partial a} = -2\sum_i X_i^{\hat{b}}\left(Y_i - \hat{a}X_i^{\hat{b}}\right) = 0$$

$$\frac{\partial SS(a,b)}{\partial b} = -2\sum_i \log(X_i)\hat{a}X_i^{\hat{b}}\left(Y_i - \hat{a}X_i^{\hat{b}}\right) = 0,$$

which illustrates their intractable nature, i.e. the equations cannot easily be solved for $\hat{a}$ and $\hat{b}$. Numerical iterative methods are required to find the least-squares solution. See, for example, Seber and Wild (1989) for an introduction to non-linear regression.

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