Scope for quantitative bioeconomics

Sebastiaan A.L.M. Kooijman, 2016/06/10
Dept. of Theoretical Biology, VU University Amsterdam, bas.kooijman@vu.nl

Abstract

Since economic systems are living, the organisation of viable economic systems might show similarities with that of living systems, which has been shaped by 3.5 billion years of evolutionary testing. Such similarities can be expected between firms and individual organisms, but also at higher levels of organisation, including interactions and the macro-level. This note presents aspects of the well-tested Dynamic Energy Budget theory for the processes of uptake and use of substrates by individual organisms that might have relevance for economic systems.

Key Words: Dynamic Energy Budget theory, conservation laws, homeostasis, κ-rule, levels of organisation, bioeconomy.

1 Introduction

People who are looking for new materials are often productively inspired by bio-materials, which were created and shaped during 3.5 billion years of evolutionary testing and selection for particular properties. Could a similar study in economic organisation be equally inspiring? I don't know the answer, but I do know that if you don't try, you will never know. Anyhow, in view of the unpredicted recent economic crises, a better and mechanistic understanding of economic processes could be useful, I would think. While life on earth exists since 3.5 billion years, the human species exists since less than 1 million, and economic systems for only few millennia at most, which are facts worth keeping in mind.

A former PhD-student of me, Tânia Sousa, still working in a group of engineers in Lisbon, tried to find where biology and economy meet common ground, and proposed formal links between these disciplines (Sousa 2007), based on the idea that both individual organisms and firms face similar (thermodynamic) constraints in their operation. I was behind the table at her defence when a neighbouring economist said to me: 'I didn't know that living systems are economic'. I answered: 'I don't think that they are, but economic systems are living'. They have similarities in how the environment selects on their inputs and outputs, including environmental interactions such as competition, predation, symbiosis, parasitism. Some species are specialists, i.e. living of a single type of resource, others are generalists. Individuals can split up into individuals with different properties, and evolution is full of examples of merging of different individuals into a single one as ultimate result of a symbiotic relationship, not unlike the dynamics of firms. Apart from these interactions between individuals and their environment, there are similarities between the internal organisation of individuals and firms. I also see similarities in the relationships between levels of organisation (micro- vs macro-economy, compared to individuals-populations-ecosystems-system earth, Nisbet et al 2000), at least in terms of problems. Where the macro-level results from the micro-level plus interactions, it is hardly productive to try to understand the macro-level

directly in this way and there is a need to delineate in-between-levels and aggregate and simplify while stepping up. Other processes become important at macro-level: time-space scales are different for the micro- and macro-levels and most processes are important in the limited range of scales only.

My background is in theoretical biology and I spend most of my academic life studying the dynamics of substrate uptake and use by organisms. They turn out to follow definite rules for this, which I captured in the Dynamic Energy Budget (DEB) theory (Kooijman 2001, 2010, Sousa et al 2008). I started to work on this theory in 1979 and it is still developing and the number of applications in the various fields is still extending (Meer et al 2014); think for instance of (eco)toxicology, pharmacology, medicine, global change, biotechnology, farming, aqua-culture, sewage water purification. The word 'Dynamic' refers to the full life cycle (or better phrased: full life trajectory) of an individual, which can be a bacterial cell, a plant or an animal, any individual that lives; This is to distinguish it from the traditional 'static' approach that does not include this aspect, and uses an administrative snapshot of energy fluxes. The word 'Energy' suggests that the focus is on energy only, but that is incomplete; it can also be chemical elements, mostly carbon, hydrogen, oxygen and nitrogen (and their isotopes, Pecquerie et al 2010). The word 'Budget' refers to the central role of conservation laws and the focus on fluxes.

Its users include ecologists, physiologists, engineers, mathematicians, chemists, physicists. The theory is presently integrated in the obligatory part of some biological and engineering university programs. Over 500 publications on this theory and its applications appeared meanwhile, in a wide scope of journals. Many classic empirical models for a wide variety of biological phenomena turn out to be special cases of DEB theory, or very good numerical approximations of it. Because of this, and the many tests against experimental data that we did ourselves, I dare to state that DEB theory is presently the best-tested quantitative theory in biology.

In this note I will expose some aspects of this organisation that might be of relevance to economic organisation, after a short description of the setup of DEB theory.

2 The standard DEB model

In practical applications, DEB theory works out as a collection of related mathematical models, of which the standard DEB model is the simplest non-degenerated one (= canonical form): one type of substrate (food), one reserve, one structure, no changes in shape during development (a property called isomorphy). The standard model assumes that the only relevant environmental variables are food availability and temperature, which might vary in time.

DEB theory can handle multiple types of substrate, more reserves and structures, changes in shape, more environmental variables that matter, but needless to say that models then have more parameters; only when their values are known can numerical predictions be made. The standard model applies to most animal species (which is no coincidence for reasons explained later).

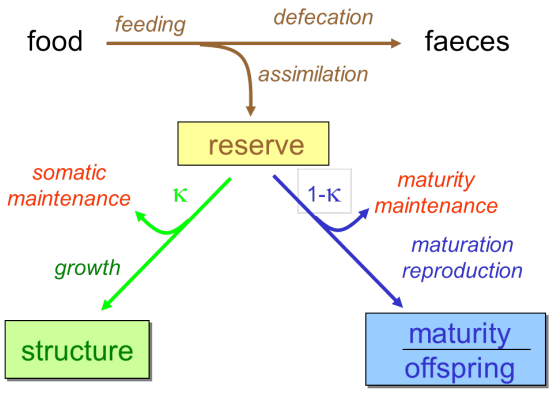

Figure 1: Energy and mass flow in the standard DEB model. After birth, food is converted to faeces and metabolites are added to reserve. A fraction κ of mobilized reserve is allocated to somatic maintenance plus growth. The rest is allocated to maturity maintenance plus maturation (before puberty) or reproduction (after puberty). Before birth, no food intake occurs and the individual starts with reserve only; structure and maturity being zero.

The setup of the standard DEB model is as follows (see figure 1). Three life stages are delineated: embryo (which does not eat), juvenile (which does not allocate to reproduction) and adult. The transition events, called birth and puberty, respectively, depend on maturity (= level of complexity), which has no matter or energy, and only the embryo and juvenile increase their maturity, adults don't. Metabolic rates depend on temperature according the (extended) Arrhenius rule. The body of the individual consists of reserve and structure in terms of matter, and of maturity and damage by ageing in terms of quality. The adult also has a reproduction buffer that is continuously filled by reserve allocation to reproduction and emptied at events by production of one or more eggs (and/or sperm). Foetal development is a variation on this pattern. Food, reserve and structure are assumed to have a constant chemical composition and thermodynamic properties, a property called strong homeostasis.

Food uptake is proportional to (structural) surface area. The individual either searches for food or processes it, while the processing time is independent of food availability. These three rules fully specify food uptake as function of food availability.

Food is converted to reserve, reserve is mobilised for metabolic use at a rate such that weak homeostasis is preserved: reserve density, defined as the ratio between reserve and structure, remains constant in juveniles and adults if (and only if) food availability remains constant. This property fully specifies reserve mobilisation.

A fixed fraction, called κ, of mobilised reserve is allocated to somatic maintenance plus growth of structure, the combination of endpoints that is called soma, the rest is allocated to maturity maintenance plus maturation in the embryo and juvenile, or deposited in a reproduction buffer in the adult (Lika & Kooijman 2011, Mueller et al 2012). Somatic maintenance is proportional to the amount of structure, maturity maintenance to the level of maturity. Maturity is quantified as the cumulative amount of reserve that was invested into maturity.

The embryo starts as a blob of reserve, with zero structure, maturity and damage by ageing. The initial amount of reserve of an egg is such that the reserve density at birth equals that of the mother at egg laying, a property called maternal effect.

Remarkable as it might seem, these rules fully specify uptake and use of substrates by

an individual, apart from the ageing process. Some additional rules are required, however, to specify what happens during extreme starvation and when and how the reproduction buffer is converted to eggs (buffer handling rules). The rules are rather formal, you are not supposed to understand what reserve and structure mean. Reserve does not mean 'set apart for later use', for instance. Further analysis showed that it has active metabolic functions, such as housing the machinery for growth of structure. In retrospection, i.e. given the rules, we can say: reserve and structure are the two material components of a body, structure requires (somatic) maintenance, reserve does not. The chemical composition of reserve and structure is not specified, but the rules state that they do have some particular composition and structure is formed from reserve. Since we know independently that the three dominant classes of chemical compounds in animals are proteins, carbohydrates and lipids, the implication is that both reserve and structure are (possibly different) mixtures of them. By making use of how the whole-body composition changes with food availability it is, by the way, possible to obtain the amounts and composition of reserve and structure in detail. Respiration, i.e. the use of dioxygen, to name another phenomenon, follows from the conservation rules for chemical elements, in combination with the implied assumption that only food intake limits individual's development. Metabolic products, such as heat, carbon dioxide, urine, hairs, feathers, shells, otoliths (= structures used to sense gravity, Fablet et al 2011, Pecquerie et al 2012) are formed in the overheads of assimilation, maintenance and growth.

Each of the 14 parameters of the standard DEB model (including 2 for ageing and 1 for temperature changes) relates to a single underlying process. The general idea is that individuals are dynamic systems that follow a trajectory with individual-specific constant parameter values. Individuals of the same species differ typically less in parameter values than between species. Bio-diversity is now captured in a multi-dimensional parameter space and evolution (and environmental stress) operates on parameter values.

Most work on DEB theory went into the evaluation and testing of the complex implications of this set of simple rules. As example I can mention the co-variation rules of parameter values among species, which require no extra assumptions, nor any empirical arguments (Kooijman 1986, Kooijman & Baas 2007, Lika et al 2011, 2011a). While most ecophysiological literature tries to link properties of species to their (fully-grown) body size, DEB theory recognizes that body size is not an independent variable, but a consequence of the rules for uptake and use of substrates. This was for me an eye-opener: when you don't start your reasoning fundamentally, there can be little hope that you can escape the descriptive phase of science. I see formalisation as the core of theoretical work in biology: deriving consequences of a list of assumptions using these assumptions only and nothing more.

3 Storing as cornerstone

DEB theory is unique in biology by the central role of reserve, which primarily smooths out fluctuations in resource availability and uncouples the direct link between input and use of

substrates. Think, for instance of algae in the oceans. They live in the top mixed layer of the ocean, varying in depth from a few till some 100+ metre, and once trapped below it, they sink to the bottom and die. The mixed layer is poor in nutrients, relative to the water below it. At the surface they store energy by synthesizing carbohydrates, and when the wind-induced turbulent currents brings them to the dark bottom of the mixed layer, they store nutrients. Without storing, they would not be able to grow since their local environment (on a cm scale) is either too dark or too poor in nutrients. Although the ultimate factor that controls primary (= photosynthetic) production, as it is called, is nutrient availability, the proximate controlling factor is wind, and to be more accurate: accelerating wind, when the shallow mixed layer is mixed-in with nutrient-rich deep water.

Most animal species on earth are insects. Insects have several life stages, and when you take a field guide, it is very likely to describe the last stage only, called imago. The imago of many insect species, however, does not eat or eats only nectar (mostly sugar only), which is very poor in proteins, not appropriate for egg formation. The synthesis of the material from which eggs are made is done much earlier by the larva, which allocates to reproduction, so in DEB-terms the larva is an adult. In fact the juvenile stage is frequently completely skipped in insects and the embryo becomes an adult at hatching. The imago only serves to copulate and deliver the eggs.

Not all storing is done inside the body. Many animal species defend territories in their breeding season with the main function of claiming resources for their offspring as part of parental care; time till death by starvation increases with body length. Almost all population dynamical models have the property that populations rapidly grow to a level where growth is ceased due to lack of resources (carrying capacity). This also holds for DEB-based population-models in homogeneous space: reproductive output ceases at low food levels. This starvation condition of individuals is, however, not frequently observed in nature. This simple observation shows that homogeneous space is convenient from a modelling point of view, but has unrealistic implications.

4 Survival of the fittest

Although Darwin never phrased it like this, Darwinists are extreme in their conviction that individuals that produce most offspring out-compete individuals of the same species with less offspring. They call this fitness, and there is a lot of discussion how this concept exactly relates to the number of offspring (reproduction rate, lifetime reproductive output, population growth rate, etc). A large amount of data on energetics showed, however, that, when analysed using DEB theory, this is not what animals are actually doing (see section on waste-to-hurry). More important than performance is existence: how well can a population survive bad environmental conditions? Some researchers became aware of the fact that the number of offspring does not tell the full story, and created the term 'all inclusive fitness' to identify the selection criterion. But for me this is scientifically an empty concept: what is 'all'? The number of offspring is relevant at the time scale of a generation, but this is extremely short, relative to that of evolution. One cannot ignore this huge difference in time scales

and assume that the environment remains constant, or that all individuals experience the same environment. It is easy to show theoretically that, when offspring of a fast-reproducing individual stays in its neighbourhood and inherits this property, the property rapidly goes extinct because of competition for food. The environment changes all the time, so does the direction of selection.

To illustrate the difference between short- and long-term effects, I want to mention the effects that plants have on the erosion of rocks (Kooijman 2004). With help of bacteria and fungi, plants transform rocks into soil, making life much easier for themselves in terms of nutrient availability (increasing surface area to allow nutrients to escape the rock) and storing of water in soils. They also enhance evaporation, which comes down as rain. The soil protects the underlying rock against erosion by wind, water and sun, which is slow compared to the action of plants on bare rock. On a hundred years time scale, plants prevent soil from flushing away into rivers and sea, so they reduce erosion. The problems with floods in Bangladesh directly relate to the cutting of forests on the slopes of the Himalayas. On a million years time scale, however, where it is almost sure that really strong, but very rare, storms occur, soil (with plants and all) is flushed into the sea and the effect of plants is opposite: plants promote erosion, rather then reduce it. In doing so, they became essential symbionts for organisms that live in the sea and are depending on the nutrients from the terrestrial environment: nutrients that reach the sea by rivers and wind (from deserts via dust) are used by bacteria and algae, which are at the basis of a whole marine foodweb.

5 Simplicity leads to robustness

I think that evolution selects for simplicity in organisation, which is why a simple theory as DEB theory can be that accurate in its predictions. If the organisation of an individual in terms of uptake and use of substrate is very complex, and the modification of one small element in this organisation has a large number of complex and coupled consequences, evolutionary change comes to a stand-still and the individual is not longer able to adapt to changing environments. As example I can mention metabolic networks.

Enzymes are proteins that catalyse chemical transformation and cells are organised such that all chemical transformations require enzymes. The amount of product produced by enzymes as function of their substrate depends hyperbolically on substrate availability: product formation is proportional to substrate availability for low levels, but constant for high levels. When they pass their product as substrate to another type of enzyme in a long chain of enzymes, the amount of product of the last enzyme in the chain still depends hyperbolically on the substrate availability of the first enzyme (Kooijman 1998, Kooijman & Segel 2005). The hyperbolic function is the most general function with this property: a hyperbola of a hyperbola is again a hyperbola (the sinus of a sinus is not again a sinus). I think that this is no coincidence, but an evolutionarily selected property. The number of steps in the transformation chain is of no relevance to the cell and it can easily insert more steps or take out steps in the chain without affecting the overall dynamics; a robustness property.

Another example for simplicity is that all rate parameters of the standard model depend

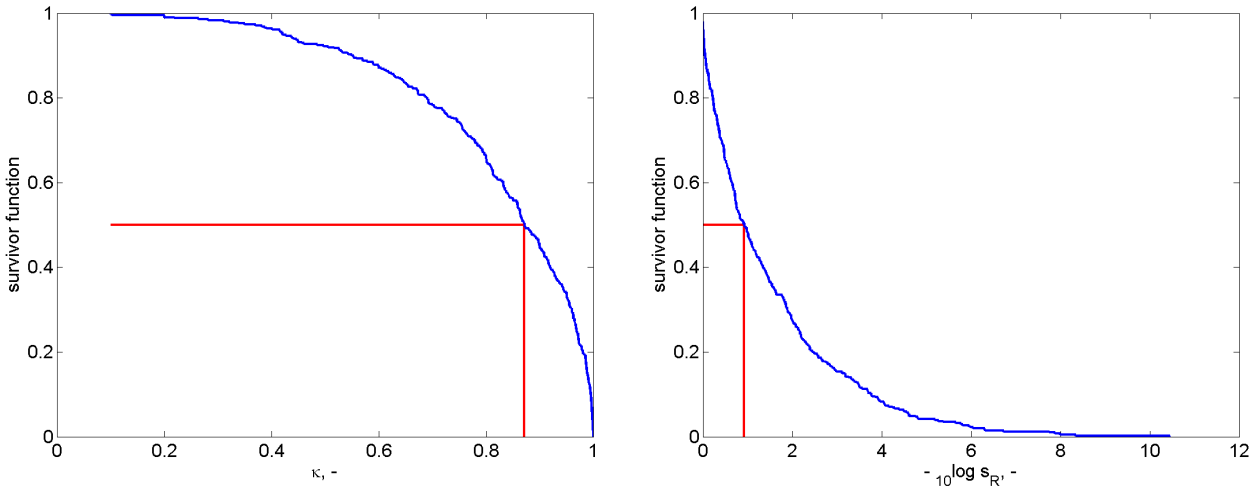

Figure 2: The survivor function of allocation fraction κ to somatic maintenance plus growth (left) and of minus the $_{10}$log of maximum reproduction as fraction s_R of the optimized maximum (right) among the 413 species in the add_my_pet collection at 2016/06/05. http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/

on temperature in the same way, with the implication that temperature affects physiological time. If assimilation would depend on temperature different from reproduction or growth, conversion efficiency (from food to structure or offspring) would depend on temperature, while the same biochemical machinery is used (and energy and mass conservation still have to apply). More complex effects of temperatures can only be incorporated in DEB models with multiple types of food, reserves and/or structures (see section on outlook).

DEB models have the remarkable (and essential) property that it is possible to merge two different individuals, both following the DEB rules with different parameter values, with incrementally small steps, such that the merged individual again follows the DEB rules (Kooijman et all 2003). This merging happened frequently in evolution as a result of a syntrophic interaction (see below); I see this as another robustness property that originates in simplicity of organisation.

6 Waste-to-hurry

Reproductive output has an optimum relationship with the allocation fraction κ of mobilised reserve to soma (= somatic maintenance plus growth). For κ close to one, little is allocated to reproduction, but for fκ close to zero is reproduction also little, because food intake is proportional to (structural) surface area, so if little is allocated to growth, food intake remains little and there is little to spend. Maximum reproduction depends on a number of parameters, but is in practice reached for $\kappa \simeq 0.4$. We found, however, that the median κ for over 400 species is 0.85, which means that reproduction rate is typically much less than the maximum possible one, given the other parameter values; think of factors 0.01 or even 0.001 (Kooijman & Lika 2014, see Figure **??**). Why species do this is more difficult to understand, but long-term stability at the population level might be one of the factors involved: by producing less offspring the pressure on prey populations (= resources) is less

high.

A remarkable and counter-intuitive implication of the κ-rule is that species can enhance growth and reproduction by wasting, i.e. increasing their somatic maintenance (Kooijman 2013); while 18 J/d.cm^3 is a typical specific somatic maintenance cost for structure at 20 °C, some species increase it till 1500 or even 8000 J/d.cm^3. They can do so in situations where their resources are for a short time very abundant, think of an algal bloom for waterflies, or of agricultural crops for some insects (called pests by farmers), or a fallen apple for a nematode or a dead mouse for bacteria; the typical abundance-period is a few months at most. They need to combine this strategy with another one, a torpor stage, to handle the meagre periods between blooms, where food is absent.

To understand waste-to-hurry it helps to realise that an individual needs to increase specific assimilation to enhance growth and reproduction (mass conservation). But if that would be the only thing that they do, they become whale-sized (with a life span of a century) and this is not a good strategy to exploit a short-lasting food supply. They also increase their somatic maintenance to remain small (and short-lived, as consequence of the ageing process, which is not discussed here), and use help by their offspring to exploit the abundant resources. They squeeze their life cycle to a fraction of the blooming-period of their resource, and experience no selection on efficiency during that period.

The waste-to-hurry scenario is in fact very common. Many animal species tend to synchronise their reproductive period with the seasons such that the (short) period of rapid growth coincides with food abundance. Grass and other plants are only rich in proteins during fast growth in spring in temperate climates or in the rainy season in the tropics. Young grazing fast-growing animals need a lot of proteins; their fully-grown parents mostly need energy and do well on protein-poor food. So it makes sense for grazing animals to squeeze their period of fast growth into the growth-season of their food. Predators (= animal-eating-animals) tend to synchronize their reproduction with that of their grazing prey, because it is easier (and less risky) to catch young animals which are also more abundant. Here control is not in the composition of food, but in its abundance only. This is why waste-to-hurry has very fuzzy boundaries and is not always easy to recognize.

If, on a multiple generation time scale, population size is (more or less) constant, each individual replaces itself 'exactly' during its full life cycle. This means that survival of the juvenile period must be bleak in species with a high reproduction rate. Ray-finned fish push this to the extreme: it is for them not unusual to produce millions of tiny eggs in the spawning season. They make quite a shift in the type of food that they take during their growth from a few mm, to the adult stage. Their food as adult typically consists of animals that feed on their offspring (Kooijman & Lika 2014a); a remarkable form of feeding their own food, which invites for contemplation about the detailed nature of prey-predator systems.

7 Deep rest

A typical life span of a species is 10 million years, but variations are large. I see the ability to survive bleak periods as the most important selection criterion for preventing extinction.

A property that typically controls the geographic distribution (Kearney 2011) and probably the life span of a species. This applies to individuals, but obviously with population consequences. While the stomach-gut system already does some smoothing of fluctuations in resource availability for animals, reserve does it much better. To find the maximum starvation time that can be bridged with reserve, we have to look for big-bodied species, since DEB's co-variation rules for parameter values expect that this time scales with body length. Blue whales live of krill in Antarctic waters for some 5 months, swim to tropical waters without feeding, get a 2.7 ton baby, give it daily 600 litre of milk, swim back together and resume feeding after returning to their Antarctic feeding grounds; a 25000 km swim that took 7 months while starving.

Many bleak periods last too long, however, to be bridged with reserve and organisms found additional strategies to handle them. Substrate availability is frequently linked with seasonal changes in temperature. In temperate climates substrate is typically hard to find at low temperatures (winter), but in tropical climates at high temperatures (dry season). Primary production in the nutrient-poor Mediterranean sea is higher in winter than in summer (more rain in winter, more nutrients washed into the sea). By linking their metabolic rate to temperature, organisms can cope with these bleak periods: absence of resources is not a problem in absence of demands. The way their metabolic rates depend on temperature deviates from the simple Arrhenius relationship and is much lower outside a species-specific temperature range.

Many species have life stages that are meant to survive bleak periods and have very low maintenance needs, or can switch to a torpor state (= deep rest). Seeds of some plant species can stay dormant for very long periods; a century is not an exception. Other species found alternative strategies to solve the same problem: migration. Terns breed in near the Arctic in the summer, but before winter arrives, fly to Antarctic areas and breed there again in Antarctic summer, so twice per year. Even much smaller butterfly species, for instance, can migrate over amazing distances.

8 Supply-demand spectrum

A supply system is very flexible in terms of growth and reproduction, which fully depend on food availability, jellyfish for example. A demand system 'wants' (via hormonal control) to grow and reproduce in particular patterns (namely what supply-species show at abundant food) and eats what it needs, birds and mammals for example. Demand systems evolved from supply systems and developed an advanced behavioural and sensorial repertoire to find the food that they need. The food density at which food intake is half of the maximum (of an individual of that size) is called the half saturation constant. If food density is larger than, say, 10 times the half saturation constant, food intake is independent of food density. Demand systems push the half saturation constant to (close to) zero, a property that I called acquisition homeostasis. Homeostasis means the ability to run metabolism as independently as possible from environmental conditions; this note mentioned several types of homeostasis already. Since resources remain essential, this 'ideal' can never be reached, but it is striking

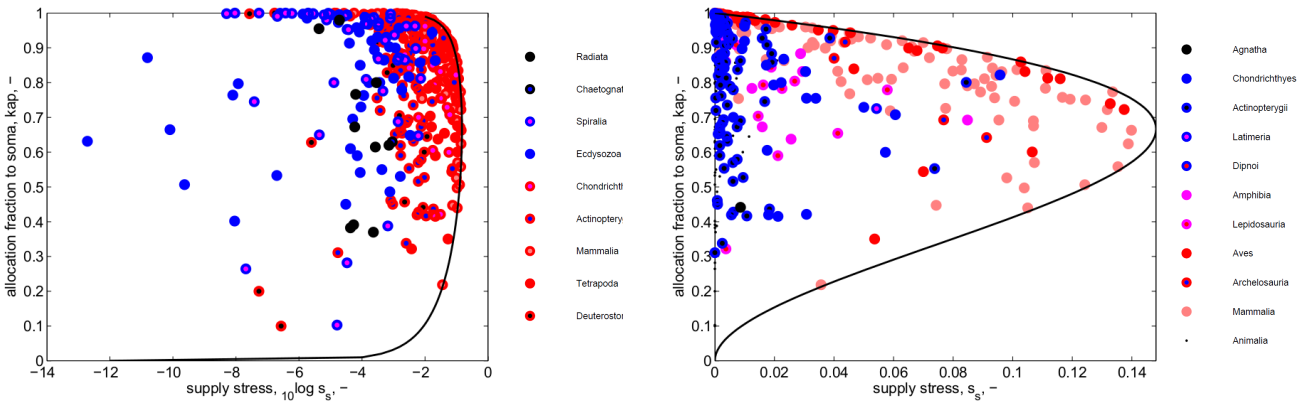

Figure 3: Allocation fraction κ as function of supply stress s_s for 411 species of the add_my_pet collection. Modified from Lika et al 2014. Notice that ecdysozoans are extreme supply species and endotherms (birds, mammals) extreme demand species. The points in both plots are identical, only the colour-coding is different and the abscissa is logarithmically transformed (left) to expose extreme supply species.

how far organisms can press this.

Quite a few properties of species are linked to their position in the supply-demand spectrum (Lika et al 2014, see Figure 3). Demand species have a high peak metabolism, relative to the standard one, with consequences for the internal transport system (a closed circulatory system, compared to an open one for supply species) and embryonic development. The standard DEB model combines supply and demand elements: growth and reproduction have a supply-organisation, while somatic and maturity maintenance have a demand-organisation; maintenance needs don't depend on substrate availability, and, as consequence, take priority over growth and maturation or reproduction. DEB theory has a quantifier for the position of species on the supply-demand spectrum: the supply-stress. It is the product of maturity maintenance and squared somatic maintenance, divided by cubed assimilation. This dimensionless compound parameter (= a function of primary parameters) can take values between 0 (supply-end of the spectrum) and 4/27 (demand-end), but no species lives at these boundaries. Parameters of over 400 animal species have been estimated from data, with mostly very high goodness of fit. It is remarkable how well the various taxonomic groups segregate along the supply-demand spectrum.

Insects are extreme supply systems, because they keep maturity maintenance low by skipping the juvenile stage. Maturation ceases at birth already, and maturity maintenance is proportional to maturation.

Birds and mammals are the demand-champions among animal species and they also control their body temperature at a constant level: thermal homeostasis. No species exists that combine high supply-stress with a small body-size. The reason might be that heating of

the body (high activity) is part of the strategy to find the required food at low food densities; heat-loss is a problem for small-bodied species. So thermal and acquisition homeostasis are coupled.

9 Metabolic acceleration

Starting to feed is complex, where help from gut-microflora is involved which first has to settle, production of a variety of digestive enzymes must be initiated, knowledge must be acquired of what to eat and what to leave alone and of how to find or catch food. If metabolism is slow initially, food intake can be low to meet the demands and more time is available to acquire the required skills for feeding and digestion.

This might be the explanation for why some animal species accelerate their metabolism after birth for some period (Kooijman et al 2011, Kooijman 2014, Lika at al 2014): they start slow and later develop more rapidly by deviating from strict isomorphy, where surface area (relevant for food uptake) is proportional to volume (relevant for somatic maintenance) to the power 2/3. They change in shape for some period, such that surface area is proportional to volume.

Extreme demand systems, such as birds and mammals, don't accelerate but found other methods to solve the same problem: parental care. They not only teach their offspring what to eat and how to catch it, but also inoculate their gut flora. Mother mammals give babies gut bacteria in their milk; a remarkable ability given how immune systems work.

10 Mutual syntrophy

Syntrophy is the phenomenon that one partner lives of the waste-products of another one. Sometimes only 2 partners are involved, such as coral polyps that house algae in their body. They live in nitrogen-poor environments, where algae have problems with extracting nitrogen directly from the water. When the polyp catches a shrimp (which is rich in protein, thus in nitrogen), the nitrogen is a waste-product for the polyp, and if the algae would not consume it, the polyp has to excrete it into the environment. The algae, on their turn, have little application for the (energy-rich) carbohydrate that they produce photosynthetically (because it is too much relative to the nitrogen that they have, for synthesizing proteins), so they excrete it and the polyp can cover part of its energy needs with it. Think also of a tree that sheds its leaves once per year (leaves loose their photosynthetic ability, also in the tropics); the soil micro-flora digests them and excretes waste-nutrients, which the tree can use for growth. Sometimes more partners are involved and syntrophy is more difficult to recognize.

DEB theory views syntrophy as a special case of partitioning and merging of metabolic fluxes, for which it uses the concept of Synthesizing Units (SUs). SU dynamics is a modification and extension of enzyme kinetics (Kooijman 1998, Kooijman & Segel 2005): it is flux-based, while enzyme kinetics works with concentrations of substrate, and neglects back-

ward fluxes, from products to substrate. This concept is used in many places in DEB theory, such as the quantification of (social) behaviour, feeding (on different food types), interaction between different reserves (in multiple-reserve systems), adaptation, co-metabolism. The feeding module of the standard model also follows SU rules, but there its properties are degenerated and difficult to recognize.

Although Darwin thought that competition is the most important driving force behind evolution, I think it is syntrophy (Kooijman & Hengeveld 2005). DEB theory shows that syntrophic interactions are dynamically very stable, no partner can outgrow the other one. Although syntrophy is generally seen as a basis for symbiosis (= living together to the benefit of all partners), the definition of symbiosis involves the concept 'benefit', which implies the existence of an aim (beneficial for what?). I doubt nature has aims, so I am unhappy with this symbiosis-concept and try to avoid thinking in terms of benefits and evolutionary success.

11 Evolution and system earth

So far the focus was on the most simple DEB model, the standard one. Single-reserve systems, however, evolved from multiple-reserve systems by the coupling of the various essential chemical compounds in the uptake (Kooijman & Troost 2007). The number of reserves that is required equals the number of independently acquired essential substrates, which differs between plants, that need several types of nutrient and typically, but not always, light, and animals that live off other organisms that already did the coupling of nutrients for them.

When an animal species lives off another animal species, conversion efficiency is high, since the relative abundance of all required chemical compounds matches exactly. When they live off plants, however, which have a different and more variable composition, the match is less close and the conversion efficiency is less. This is why a cow eats that much grass: with help of their gut-flora, the cow finds lots of energy in grass, but little proteins. So a single-reserve system responds to mismatches between supply and demand in terms of composition, by decreasing overall digestion efficiency.

While plants evolved from bacteria by increasing metabolic flexibility, animals became metabolically less flexible but behaviourally more complex. Moreover these groups became increasingly depending on each other in a world-wide metabolic network that affected the development of system earth (Kooijman 2004, Kooijman & Hengeveld 2005).

12 Outlook

We did quite a bit research on finding alternatives for the standard DEB model. None of the 20 possible topological alternatives with the same state variables could capture a number of empirical stylized facts (Lika & Kooijman, 2011). But even if one would allow different state variables, I don't expect that alternatives for the standard DEB model will ever be found with an equal level of simplicity and generality. I see possibilities for alternatives only for (substantially) more complex models, measured in number of parameters and state variables.

My motivation for this expectation rests on consistency arguments: the more simple models become, the more constraining consistency requirements become. As soon as one formulates a model that applies to some species, but not to others, there is a need to delineate for which species and to specify models for the other species such that it is consistent with evolutionary history, where all species have a common ancestor. Likewise, if the models for embryos, juveniles and adults would have a different structure, there is a need to specify what causes the transitions and to explain how this can be done with the same biochemical machinery.

I don't think that energy and mass conservation count as assumptions, but actively exploiting them, like DEB theory does, is another issue. Only in this way, one can quantify the entropy of living matter and fully determine thermodynamically what is going on (Sousa et al 2006). Since the number of chemical compounds in living cells is very large, mass balances cannot be respected in (simple) models that follow particular compounds, and one is forced to delineate a small number of metabolic pools (such as reserve(s) and structure(s) in DEB theory) and assume strong homeostasis. This is why the degrees of freedom to formulate simple consistent models is really restricted.

In this short introduction, I focussed on biological aspects only. The analysis of similarities and differences between biological and economic processes is in itself a substantial field of research. I hope that this note motivates investment into this field.

More information about the DEB research program can be found at the DEB information page (including bibliography, DEB (tele)course, DEB laboratory), http://www.bio.vu.nl/thb/deb, and the DEB wiki, http://www.debtheory.org/.

Acknowledgements

I want to thank Tânia Sousa and Tiago Domingos for the many years of inspiring discussions on this issue and their constructive comments on this note. I also wnat to thank Alain Wouters for his helpful comments.

References

R. Fablet, L. Pecquerie, H De Pontual, H. Hoie, R. Millner, H. Mosegaard, and S. A. L. M. Kooijman (2011). Shedding light on fish otolith biomineralisation using a bioenergetic approach. *PLosOne*, 6:e27055.

M. R. Kearney (2011). Metabolic theory, life history, and the distribution of a terrestrial ectotherm. *Functional Ecology*, 26:167–179.

S. A. L. M. Kooijman (1986). Energy budgets can explain body size relations. *J. Theor. Biol.*, 121:269–282.

S. A. L. M. Kooijman (1998). The synthesizing unit as model for the stoichiometric fusion and branching of metabolic fluxes. *Biophys. Chem.*, 73:179–188.

S. A. L. M. Kooijman (2001). Quantitative aspects of metabolic organization; a discussion of concepts. *Phil. Trans. R. Soc. B*, 356:331–349.

S. A. L. M. Kooijman (2004). On the coevolution of life and its environment. In S. H. Schneider, J. R. Miller,

E. Crist, and P. J. Boston, editors, *Scientists Debate Gaia; the next century.*, chapter 30, pages 343–351. MIT Press, Cambridge, Mass.

S. A. L. M. Kooijman (2010). *Dynamic Energy Budget theory for metabolic organisation.* Cambridge University Press. Comments on this book: `http://www.bio.vu.nl/thb/research/bib/Kooy2010_c.pdf`.

S. A. L. M. Kooijman (2013). Waste to hurry: Dynamic energy budgets explain the need of wasting to fully exploit blooming resources. *Oikos*, 122:348–357.

S. A. L. M. Kooijman (2014). Metabolic acceleration in animal ontogeny: an evolutionary perspective. *J. Sea Res.*, 94:128–137.

S. A. L. M. Kooijman, P. Auger, J. C. Poggiale, and B. W. Kooi (2003). Quantitative steps in symbiogenesis and the evolution of homeostasis. *Biol. Reviews*, 78:435–463.

S. A. L. M. Kooijman, J. Baas, D. Bontje, M. Broerse, T. Jager, C. A. M. van Gestel, and B. van Hattum (2007). Scaling relationships based on partition coefficients and body sizes have similarities and interactions. *SAR and QSAR in Environ. Res.*, 18:315–330.

S. A. L. M. Kooijman and R. Hengeveld (2005). The symbiontic nature of metabolic evolution. In T. A. C. Reydon and L. Hemerik, editors, *Current Themes in Theoretical Biology: A Dutch perspective.*, pages 159–202. Springer, Dordrecht.

S. A. L. M. Kooijman and K. Lika (2014). Resource allocation to reproduction in animals. *Biol. Rev.*, 89:849–859.

S. A. L. M. Kooijman and K. Lika (2014a). Comparative energetics of the 5 fish classes on the basis of Dynamic Energy Budgets. *J. Sea Res.*, 94:19–28.

S. A. L. M. Kooijman, L. Pecquerie, S. Augustine, and M. Jusup (2011). Scenarios for acceleration in fish development and the role of metamorphosis. *J. Sea Res.*, 66:419–423.

S. A. L. M. Kooijman and L. A. Segel (2005). How growth affects the fate of cellular substrates. *Bull. Math. Biol.*, 67:57 – 77.

S. A. L. M. Kooijman and T. A. Troost (2007). Quantitative steps in the evolution of metabolic organisation as specified by the Dynamic Energy Budget theory. *Biol. Reviews*, 82:1–30.

K. Lika, S. Augustine, L. Pecquerie, and S. A. L. M. Kooijman (2014). The bijection from data to parameter space with the standard DEB model quantifies the supply-demand spectrum. *J. Theor. Biol.*, 354:35–47.

K. Lika, M. R. Kearney, V. Freitas, H. W. van der Veer, J. van der Meer, J. W. M. Wijsman, L. Pecquerie, and S. A. L. M. Kooijman (2011). The 'covariation method' for estimating the parameters of the standard Dynamic Energy Budget model I: philosophy and approach. *J. Sea Res.*, 66:270–277.

K. Lika, M. R. Kearney, and S. A. L. M. Kooijman (2011). The 'covariation method' for estimating the parameters of the standard Dynamic Energy Budget model II: properties and preliminary patterns. *J. Sea Res.*, 66:278–288.

K. Lika and S. A. L. M. Kooijman (2011). The comparative topology of energy allocation in budget models. *J. Sea Res.*, 66:381–391.

K. Lika, S. A. L. M. Kooijman, and N. Papandroulakis (2014). Metabolic acceleration in mediterranean perciformes. *J. Sea Res.*, 94:37–46.

J. van der Meer, C. Klok, M. R. A. Kearney, J. W. M. Wijsman, and S. A. L. M. Kooijman (2014). 35 years of deb research. *J. Sea Res.*, 94:1–4.

C. Mueller, A. Augustine, S. A. L. M. Kooijman, M. R. Kearney, and R. Seymore (2012). The trade-off between maturation and growth during accelerated development in frogs. *Comp. Physiol. Biochem. A*, 163:103–110.

R. M. Nisbet, E. B. Muller, K. Lika, and S. A. L. M. Kooijman (2000). From molecules to ecosystems through dynamic energy budget models. *J. Anim. Ecol*, 69:913–926.

L. Pecquerie, R. Fablet, P. Petitgas, M. Alunno-Bruscia, and S. A. L. M. Kooijman (2012). Reconstructing individual food and growth histories from calcified structures of acquatic organisms. *Mar. Ecol. Prog. Ser.*, 447:151–164.

L. Pecquerie, R. M. Nisbet, R. Fablet, A. Lorrain, and S. A. L. M. Kooijman (2010). The impact of metabolism on stable isotope dynamics: a theoretical framework. *Phil. Trans. R. Soc. B*, 365:3455–3468.

T. Sousa (2007). *Thermodynamics as a Substantive and Formal Theory for the Analysis of Economic and Biological Systems*. PhD thesis, Technical University Lisbon & VU University Amsterdam.

T. Sousa, T. Domingos, and S. A. L. M. Kooijman (2008). From empirical patterns to theory: A formal metabolic theory of life. *Phil. Trans. R. Soc. B*, 363:2453–2464.

T. Sousa, R. Mota, T. Domingos, and S. A. L. M. Kooijman (2006). The thermodynamics of organisms in the context of Dynamic Energy Budget theory. *Physical Review E*, 74(051901):1–15.