



INSTITUTO SUPERIOR TÉCNICO  
Universidade Técnica de Lisboa

# **MECHANISTIC ANALYSIS OF ENERGY AND ENTROPY IN BIOLOGICAL AND ECOLOGICAL SYSTEMS**

**João Diogo Costa Fernandes**

Dissertação para obtenção do Grau de Mestre em  
**Engenharia do Ambiente**

## **Júri**

Presidente: Professor Doutor Tiago Morais Delgado Domingos  
Orientador: Professora Doutora Tânia Alexandra dos Santos Costa e Sousa  
Co-orientador: Professor Doutor Tiago Morais Delgado Domingos  
Vogais: Professor Doutor António Domingos Heitor da Silva Reis  
Professor Doutor Francisco André Campos Pereira Dionísio

**Novembro de 2008**



## **Acknowledgments**

First, I would like to thank Tânia Sousa and Tiago Domingos for their insightful orientation and guidance. I would also like to thank Bas Kooijman for the constructive suggestions and critical contributions. With such robust shoulders to stand upon, this work seemed less daunting.

Of course, this work would be much more incomplete without the support and camaraderie of all the people going through the same enduring experience: I would like to thank André Serrenho, Nuno Rodrigues, Catarina Henriques, António Lorena, João Machado, Filipe Sousa, Rita Candeias, Ana Magina, Maria Saião, Gonçalo Guerreiro, and all the others that managed to survive the last months. In a wider group, my thanks also go out to all friends that, consciously or not, made sure sanity would prevail.

Most importantly, I would like to thank my family for their patience, support and for taking the time to have vacations even when others couldn't.

Last but not most, thank you, Joana, because I truly couldn't have done it without you.



## Resumo

A vida tem raízes profundas nas limitações de disponibilidade de energia e massa. O metabolismo, definido como o conjunto de reacções e fluxos que os sistemas vivos gerem de forma a se manterem, cumpre um papel fundamental no controlo daquelas limitações.

Este enquadramento geral pode ser aplicado a qualquer escala em que comportamentos de manutenção e reprodução surjam, conhecidos geralmente como estruturas dissipativas. Para a vida biológica, exemplos destas entidades vão da célula ao ecossistema.

Neste trabalho, é apresentada uma síntese bibliográfica de aplicações termodinâmicas relevantes para um ecossistema genérico abordando os processos de crescimento e desenvolvimento. Por outro lado, é dada especial atenção a relações de escala ao nível individual com o uso de uma teoria geral, a teoria *Dynamic Energy Budget*, em comparação com relações de escala alométricas, mais usuais na literatura. A teoria é usada para verificar determinados resultados em comparações intra e inter-espécie, em particular sobre taxas metabólicas, produção de entropia, e intervalos de tempo fisiológicos.

Os resultados deste trabalho apontam para a importância de obter explicações fundamentadas teoricamente e do uso cuidadoso de conceitos agregados, e evidenciam a semelhança holística entre ecossistemas e organismos. De uma forma geral, as regras alométricas adequam-se mas não explicam o comportamento das variáveis, tipicamente relacionados com um compromisso entre proporcionalidade com o volume e com a área. Conclui-se que a produção de entropia num organismo é afectada principalmente pelo uso dissipativo de energia em custos de manutenção e em investimento em diferenciação.

**Palavras-chave** metabolismo, teoria *Dynamic Energy Budget*, estruturas dissipativas, entropia

## **Abstract**

Life has deep roots in energy and mass availability limitations. The metabolism, defined as the set of reactions and fluxes living systems manage in order to maintain themselves, plays an important role in dealing with those limitations.

This general framing can be theoretically applied to any scale at which self-maintaining and self-reproducing behaviours, generally known as dissipative structures, arise. For biological life, examples of such entities go from the cell to the multilayered ecosystem.

In this work, a bibliographical synthesis is presented for the thermodynamic applications relevant for a general ecosystem, in particular for the growth and development. On the other hand, special attention is given to the individual-level scaling rules, with the use of a general biological theory, Dynamic Energy Budget theory, in comparison with more usual allometric scaling laws. The theory is used to verify certain results in intra- and inter-species comparisons, regarding metabolic power rate, the production of entropy, and physiological time lapses.

The results of this work point to the importance of theoretically sound explanations and of careful use of aggregative concepts, and show the holistic similarity between ecosystems and organisms. Generally, the allometric scaling laws are adequate but do not explain in depth variable behaviour, which is typically related to compromises between volume and surface proportionality. It is concluded that entropy production by an organism is majorly affected by the dissipative use of energy in maintenance costs and investment in differentiation.

**Keywords** metabolism, Dynamic Energy Budget theory, dissipative structures, entropy

# Contents

<b>1</b>	<b>Introduction</b>	<b>1</b>
<b>2</b>	<b>Energy in biological and ecological systems</b>	<b>3</b>
2.1	Thermodynamics . . . . .	3
2.1.1	Exergy . . . . .	5
2.1.2	Emergy . . . . .	6
2.1.3	Dissipative structures . . . . .	8
2.2	Ecological systems . . . . .	9
2.2.1	Ecological goal functions . . . . .	11
2.3	Biological systems . . . . .	15
2.3.1	Quantification and quality . . . . .	15
2.3.2	Allometry . . . . .	16
<b>3</b>	<b>Dynamic Energy Budget theory</b>	<b>21</b>
3.1	General description . . . . .	21
3.1.1	Metabolic schematics . . . . .	24
3.2	Model description . . . . .	26
3.2.1	Physiological time . . . . .	31
3.2.2	Metabolic rates . . . . .	31
3.2.3	Mass fluxes, respiration and dissipated heat . . . . .	35
<b>4</b>	<b>Applications</b>	<b>39</b>
4.1	Intra-species results . . . . .	40
4.2	Inter-species results . . . . .	49
4.3	Sensitivity analysis . . . . .	55
4.3.1	Intra-species analysis . . . . .	55
4.3.2	Inter-species analysis . . . . .	62
<b>5</b>	<b>Discussion</b>	<b>65</b>
<b>6</b>	<b>Concluding Remarks</b>	<b>69</b>

## List of Tables

1	Stylized facts explained by DEB theory. . . . .	22
2	Assumptions for full standard DEB model specification. . . . .	23
3	Parameter description for a 1-E, 1-V, 3-S isomorph in DEB. . . . .	27
4	Compound parameters description. . . . .	27
5	Parameter conversions for a reference species. . . . .	28
6	Mineral and organic components' chemical composition, chemical potential, molar enthalpies and molar entropies. . . . .	29
7	Power rate expressions for the modelled organism. . . . .	34
8	Dioxygen, dissipated heat, and entropy production couplers for the assimilation, dissipation, and growth processes. . . . .	36
9	Extreme values used for the sensitivity analysis . . . . .	55
10	Extreme values used for $\dot{k}_M$ sensitivity analysis and resultant $\dot{p}_C$ allometric approximation exponents . . . . .	56
11	Extreme values used for $\kappa$ sensitivity analysis and resultant $\dot{p}_C$ allometric approximation exponents . . . . .	58
12	Extreme values used for $l_b$ and $l_p$ sensitivity analysis and resultant $\dot{p}_C$ allometric approximation exponents . . . . .	61
13	Parameter for obtained power law fits to variable evolution . . . . .	65

## List of Figures

1	Metabolic allocation schematics . . . . .	24
2	Wet weight vs. structural volume for varying reserve densities for the intra-species comparison . . . . .	40
3	Assimilation, dissipation, and growth power rates vs. wet weight for the intra-species comparison . . . . .	41
4	Dioxygen consumption rate vs. wet weight for the intra-species comparison . . . . .	42
5	Power rates $\dot{p}_A$ and $\dot{p}_C$ vs. wet weight for the intra-species comparison . . . . .	43
6	Power rates $\dot{p}_D$ and $\dot{p}_{T+}$ vs. wet weight for the intra-species comparison . . . . .	43
7	Absolute entropy production vs. wet weight for the intra-species comparison . . . . .	44



8	Specific entropy production vs. wet weight for the intra-species comparison . . .	45
9	Contributions towards total entropy production vs. wet weight for the intra-species comparison . . . . .	46
10	Reserve residence time vs. wet weight for the intra-species comparison . . . .	47
11	Specific entropy production in a reserve residence time lapse vs. wet weight for the intra-species comparison . . . . .	48
12	Power rates $\dot{p}_A = \dot{p}_C$ , $\dot{p}_D$ , and $\dot{p}_{T+}$ vs. wet weight for the inter-species comparison . . . . .	49
13	Absolute entropy production vs. maximum wet weight for the inter-species comparison . . . . .	51
14	Specific entropy production vs. maximum wet weight for the inter-species comparison . . . . .	51
15	Contributions towards total entropy production vs. wet weight for the intra-species comparison . . . . .	52
16	Reserve residence time vs. maximum wet weight for the inter-species comparison . . . . .	53
17	Specific entropy production in a reserve residence time lapse vs. maximum wet weight for the inter-species comparison . . . . .	54
18	Catabolic power vs. wet weight for three different values of $\dot{k}_M$ . . . . .	56
19	Specific entropy production vs. wet weight for three different values of $\dot{k}_M$ . . .	57
20	Catabolic power vs. wet weight for three different values of $\kappa$ . . . . .	58
21	Specific entropy production vs. wet weight for three different values of $\kappa$ . . . .	59
22	Specific entropy production vs. wet weight for three sets of parameters . . . .	60
23	Dioxygen consumption flux vs. wet weight for the three sets of values of $l_b$ and $l_p$ . . . . .	61
24	Catabolic power vs. wet weight for three different values of $\dot{k}_M$ for the inter-species comparison . . . . .	62
25	Catabolic power vs. wet weight for three different values of $\kappa$ for the inter-species comparison . . . . .	63

## Notations and symbols

### Abbreviations

BMR	Basal Metabolic Rate
DEB	Dynamic Energy Budget
DNA	Deoxyribonucleic Acid
MMR	Maximum Metabolic Rate
MTE	Metabolic Theory of Ecology
$CO_2$	Carbon dioxide
$H_2O$	Water
$O_2$	Dioxygen
$NH_3$	Ammonia

Dimension	Symbol	Unit
Energy	$\mathcal{E}$	J
Temperature	$\mathcal{T}$	K
Time	$t$	d
Length	$l$	cm
Number	#	mol
Mass	$M$	g
Volume specific *	[*]	*.cm <sup>-3</sup>
Surface specific *	{*}	*.cm <sup>-2</sup>
Time specific *	⋆	*.d <sup>-1</sup>
Vectors and matrixes $X$	$\mathbf{X}$	–
Transpose $X$	$\mathbf{X}^T$	–

DEB Variables	Symbol	Dimension	Expression
Food	$X$	$\#.l^{-3}$	
Structure	$V$	$l^3$	
Reserve	$E$	$\mathcal{E}$	
Product	$P$	$\#.l^{-3}$	
Scaled functional response	$f$	$-$	$X. (K_X + X)^{-1}$
Scaled length	$l$	$-$	$\frac{L}{L_m}$
Scaled reserve density	$e$	$-$	$\frac{[E]}{[E_m]}$
Energy flux of process *	$\dot{p}_*$	$\mathcal{E}.t^{-1}$	
Flux of compound *	$\dot{J}_*$	$\#.t^{-1}$	
Wet weight	$W_w$	$M$	
Entropy production	$\dot{\sigma}$	$\mathcal{E}.\mathcal{T}^{-1}.t^{-1}$	
Reserve residence time	$t_E$	$t$	$\frac{E}{\dot{p}_C}$
Half saturation coefficient	$K_X$	$\#.l^{-3}$	
Mass *1 to energy *2 coupler	$\eta_{*1*2}$	$\#.\mathcal{E}^{-1}$	
Energy *2 to mass *1 coupler	$\mu_{*2*1}$	$\mathcal{E}.\#^{-1}$	
Mass *1 to mass *2 coupler	$y_{*1*2}$	$-$	
Molar weight of compound *	$w_*$	$M.\#^{-1}$	
Density of compound *	$d_*$	$M.l^{-3}$	
Molar enthalpy for compound *	$\bar{h}_*$	$\mathcal{E}.\#^{-1}$	
Molar entropy for compound *	$\bar{s}_*$	$\mathcal{E}.\mathcal{T}^{-1}.\#^{-1}$	



# 1 Introduction

This work explores the connections between energy, metabolism and entropy production across scales of biological and ecological systems. For such a task, a general biological energetic behaviour description, Dynamic Energy Budget or DEB theory (Kooijman, 2009), is used to obtain representative results for the biological level, while a comprehensive bibliographic synthesis is presented for higher level ecosystems.

The goal is to give a functional multi-scale approach to energy in life, namely at the organism scale and at a more holistic ecosystem scale. In this way, important results can be translated by analogy between systems, stressing the possibly common mechanistic and formal aspects of their activities. This multi-scale analysis is forcefully limited by the availability of mechanistic theories for these systems given the scope of this work.

The emergence of systems can be attributable to available energy and resources. However, neither the concept of system nor the concept of availability have clearly bounded definitions. Nevertheless, investigation of some particular types of systems and their limits and consequences can provide interesting theoretical resources to explore successively more complex systems.

The organism and the ecosystem scales were chosen because they represent relatively coherent entities (Allen and Hoekstra, 1992), at least conceptually. While the organism is defined as a single, undividable biological system that functions independently, the ecosystem could be interpreted as an assembly of interacting individual biological systems, or organisms, and their respective biological, atmospherical, and geological spheres of influence. Hence, the ecosystem can be seen as a undividable functioning system, analogously to the organism.

Consequently, there are some systemic similarities for these two levels of biological organisation that do not arise from the fact that one concept encompasses the other. These systems share mechanistical structure, in the sense that both of them exist thanks to the mass and energy fluxes they promote with their surroundings.

For the lower level of complexity, an allometric scaling rule has been proposed by Andersen et al. (2002) for the production of entropy in biological systems. Their result leads to an interesting consequence of equivalent efficiency for all living systems, as long as evaluated on the organism's intrinsic time scale, instead of a regular outside observer time scale. This intrinsic time scale is defined as any time scale that somehow reflects the rate at which the organism reacts to external stimuli.

However, this approach has several chinks in its theoretical armour, most relating to the use of empirical allometric scaling rules. Although they yield good statistical fits to certain data sets, these rules should not replace a theoretically sound explanation. Hence the use of a general Dynamic Energy Budget (DEB) model in this work. Beyond the stronger formal

structure, this type of model benefits from substantive integration with thermodynamics, easing the path to conclusions in a meaningful way.

In addition to presenting alternative mechanistic definitions of individual metabolic processes, otherwise known as metabolic rates, this work also summarizes relevant literature on similar subjects but on a higher ecosystem scale, contributing to a possible unification across biological scales.

The goals of this work are (1) to investigate whether or not holistic ecological goals of development apply to the way individual organisms grow, (2) to present alternative measures of metabolic rate, (3) to follow the evolution of metabolic rates and entropy production in an aerobic organism during its life-cycle, (4) to uncover which types of metabolic activity produce more entropy, (5), to analyse results within a representative physiological time lapse, and (6) to compare obtained results with allometric scaling rules. These results will also be obtained, whenever possible, for intra-species and inter-species comparisons.

In chapter 2, the biological and ecological systems are approached from a general thermodynamics approach, with the particularisation of some specific tools and applicative concepts. A general analysis is made of holistic principles of ecological growth and development. In chapter 3, the Dynamic Energy Budget for biological systems is presented in general and further particularized for the analysis of an ectothermic animal during its life-cycle and for the comparison of similar species, with particular emphasis on energy transformation and use. Chapter 4 presents the model results for the different analysed variables and conditions, as well as a set of sensitivity tests for these results' stability. Finally, chapter 5 displays the discussion of the referred results and chapter 6 concludes, connecting both levels of analysis and providing a description of possible future work on these subjects.

## **2 Energy in biological and ecological systems**

In this chapter, the thermodynamic aspects of biological and ecological systems are discussed and some formal frameworks are presented for their analysis. In section 2.1 a general description of thermodynamics is made, with the presentation of some ecologically relevant concepts. Section 2.2 presents a comprehensive review and analysis of the thermodynamic approaches to ecology available in scientific literature. Finally, section 2.3 discusses the usual descriptions of low scale metabolisms.

### **2.1 Thermodynamics**

When dealing with the most varied phenomena, human knowledge depends on the invariability of some known entity. Be it philosophy, mathematics or physics, it is always easier to analyse a system if something, preferably everything but the object of study, remains invariant. In its genesis, energy arose as a property to anticipate the evolution of collision and simple kinetic problems (Mirowski, 1989). Assuming that the total energy remained unchanged and was composed ideally only by kinetic energy, the solution could be attained by differential analysis, in order to assess how much of it was converted into other forms.

Motivated by the quest for better engines, physicists developed what would later become the fundamental branch of thermodynamics. Hence, a framework of convertible forms of energy and their conversion rates was and has been gradually established. This approach expanded into every physics' branches, and even to economics, leading to major technological breakthroughs that were responsible for the rapid spreading of the industrial revolution.

Thermodynamics studies the different forms of energy and their proprieties, especially the ways in which they convert to one another. In order to simplify the analysis, a boundary is usually defined that divides the universe in system and surroundings, accounting for the energy and mass fluxes across the boundary. In this way, knowing the system's quantitative state of energy and mass is simple, given full knowledge of the flows coming out and going in. However, the same cannot be said about the quality of the system's energy, as information about the system's internal processes is key to the full description of the system's energy quality. This quality is connected with the concept of entropy, derived to explain dissipation and energy "loss" phenomena.

There are four major laws of thermodynamics, of general validity, that can be synthesized as follow:

0. If two thermodynamic systems are separately in thermal equilibrium with a third, they are also in thermal equilibrium with each other.
1. The change in the internal energy of a closed thermodynamic system is equal to the sum of the amount of heat energy supplied to the system and the work done on the system.
2. The total entropy of any isolated thermodynamic system tends to increase over time, approaching a maximum value.
3. As a system's temperature approaches absolute zero asymptotically, all processes cease and the entropy of the system asymptotically approaches zero.

By joining the first and second laws an important result of thermodynamics is obtained: the total energy of any given isolated system (i.e., without any energy or mass transference to its surroundings) is constant and becomes qualitatively poorer, as it is converted into more entropic energy forms.

In other words, the equilibrium for any given isolated system is to convert all of its energy into the most entropic energy state and to eliminate any kind of internal gradient or structure. Fundamentally, this is why internal description is essential: as the total entropy of all isolated thermodynamic systems increases in a way fully dependent on the system's states and structures, there is no way to characterize the entropy of a given system by only analysing its boundary fluxes.

Thermodynamic analysis is, according to its founding interests, particularly useful for the development, analysis and improvement of energetic systems. In particular for ecological systems, some additional concepts are introduced.

Given the importance of a reference environment in one case, and the intricate system point of view in the others, these tools are particularly relevant for holistic large scale system analysis, provided strong and clear boundaries and information about these systems are available. Although they are not subsequently used for the biological section of this work because of these limitations, the presented tools represent two interesting approaches to the thermodynamics of ecological systems.



### 2.1.1 Exergy

The amount of work extractable from any system when brought into equilibrium with its surroundings was first defined by J. W. Gibbs as “available energy of the body and medium” and was later coined as exergy. This concept is useful in analysing thermodynamic systems because it represents a measure of available energy in the system, being strictly connected to the notions of gradient and entropy.

A gradient is defined as any spatial variation in an intensive thermodynamic variable, such as temperature, pressure or chemical potential. This gradient represents available energy that can hypothetically be harnessed by an orderly re-establishment of equilibrium. When in thermodynamic equilibrium, all systems have null exergies, and correspondingly maximum entropies. However, exergy destruction is “more than a different way to represent entropy production because it inherently incorporates additional information about the system’s environment” (Kay and Fraser, 2002) and this condition imposes the need for a well defined environment, with which the system interacts, allowing for work extraction.

Conversely, the generation of gradients can only be obtained with the transformation of available energy. In fact, this allows an intuitively sound illustration of the depth of the concept of entropy: energy can be stored up in gradients, but when these gradients are later exhausted for energy withdrawal, some of the initially stored energy becomes unavailable because it is, somewhere along the process, inevitably converted into a more entropic form. Otherwise, it would be possible to indefinitely store and extract the same energy over and over, which is forbidden by the second law of thermodynamics.

Given that the presence of usable energy in systems is simultaneously the result and the promoter of the development of structure, such as otherwise unstable molecules as DNA, trees’ trunks spanning tens of meters, and laptops, exergy comes to be an essential concept for every energy dependent system.

Classical exergy only takes into account potentially extractable work, made possible by any physical gradients that can be exploitable by approaching the conditions of the reference environment. Jørgensen’s definition of ecological exergy, however, incorporates a term related to the organisational aspects of the components of a given ecological system (Jørgensen and Fath, 2004). This information is assumed to be approximated by its inhabitants’ genetic variability (Jørgensen et al., 1995); thus, ecological exergy “includes both the energy that can be turned into work and the biological information which separates the organism from its surroundings” (Jørgensen and Fath, 2004).

In this way the embodied exergy of higher biological organisation is incorporated into the concept of exergy, under the assumptions that (i) there is a correlation between the genetic variability and biological complexity and (ii) higher biological complexity represents higher capability to maintain the system far from thermodynamic equilibrium, which in other words

means higher embodied exergy.

The general expression for ecological exergy yields (Jørgensen et al., 1995)

$$\frac{Ex}{RT} = (\mu_1 - \mu_1^{eq}) \sum_{i=1}^N \frac{c_i}{RT} - \sum_{i=2}^N c_i \ln P_{i,a}, \quad (1)$$

where  $R$  is the perfect gas constant,  $T$  is the absolute temperature,  $\mu_i$  is the component  $i$ 's chemical potential,  $c_i$  is  $i$ 's concentration in the ecosystem, component 1 is dead organic matter,  $N$  is total number of ecosystem components, and  $P_{i,a}$  represents the inverse of the permutations of genetic coding for amino acids which, assuming that living organisms use 20 different amino acids and that each gene determines an average of 700 amino acids, equals

$$P_{i,a} = 20^{-700g_i}, \quad (2)$$

where  $g_i$  is the number of genes of component  $i$  (Jørgensen et al., 1995).

Although rather bluntly, these expressions allow an estimation of systemic ecological maturity by biological component analysis, by assuming certain values for  $g_i$  according to different species' nuclear DNA gene coding capacity data (Fonseca et al., 2002). Even though this formalization will not be used in this work's practical applications, it is important to be able to quantify the complexity of biological and ecological systems.

### 2.1.2 Emergy

Another thermodynamic variable was defined by Odum as emergy, specifically for ecological applications (Odum, 1996), as the sum of all available energy of any one kind used up in transformations leading up to a product or service.

As solar energy is the major energetic input into the biosphere, emergy is defined particularly for ecology as the solar equivalents (measured in  $[seJ]$ , solar embodied Joule) required to obtain a given product or service. The conversion of all other kinds of energy into the equivalent solar energy is made according to whichever conversion factors, dubbed transformities, apply (Brown and Ulgiati, 2004). The concept of emergy is then intended to evaluate the quality of the energy needed to achieve a given state: higher values of emergy result from processes with a higher amount of dissipation. This concept can be approached as an historical exergy of sorts: instead of accounting for the "usefulness" of the state itself, emergy evaluates only the processes leading to it.

Take the case of 1 Joule of electricity, for example. If this electricity is produced directly through photovoltaic harnessing it will represent lower emergy than in the case of being produced by burning of fossil fuels, wherein more embodied solar energy has to be used in

order to produce the same amount of final energy. Ideally this accounting should consider the life-cycle of all the materials and technologies needed for the production; it quickly becomes clear that a comprehensive analysis of a given product's emergy value is not by all means trivial. Contrastingly, the exergy of 1 Joule of electricity is arguably always the same, whatever the production processes leading to it may be.

Higher emergy of a given system indicates that its associated fluxes result from a more dissipative process history; however, emergy does not account for the system's inherent quality in terms of available energy. For example, while exergy only describes the properties of a given fuel, emergy only describes the processes used to obtain it. Comparably, emergy approximates what it has cost to obtain a certain subject, in terms of irreversibilities, while exergy calculates the available energy that the subject possesses in context with its environment (Jørgensen et al., 1995).

By considering the input flux of emergy per period of time, Odum derived the concept of empower (Odum, 1996). This concept is useful because it allows a gauging of the evolution of the system's "historical energy quality" needs, even if this concept is relatively intangible.

The concepts associated with emergy cannot be defined outside a functioning system. For example, while emergy is usable at the ecosystem level as a meaningful concept, for an organism it is hard to see how the ecological concept could be useful. The equivalent concept for individual organisms would only consider energy use and transformation inside the organism as an independent system, for example as embodied ATP hydrolysis energy. In this simulated example, a compound with a higher embodied ATP hydrolysis energy would come from more expensive processes. Such concept would then only be useful at complexity levels below the systemic organism, as a tool to analyse internal processing, which is beyond the scope of this work.

### 2.1.3 Dissipative structures

In the evolution of life, a tendency of aggregation of “fundamental” structures has been taking place, as can be seen by the sequence of the formation of simple molecules, biopolymers and eventually the formation of multicellular organisms. This general trend can be understood as a progressive improvement in the potential of biologic systems to dissipate incoming available inputs. This trend can also be compared to what happens with, for example, small scale convection or large scale atmospheric systems. As Kay and Fraser (2002) so synthetically put it :

“The earth is an open thermodynamic system with a large exergy flow impressed upon it by the sun. Consequently physical and chemical processes will emerge to destroy the incoming exergy. For example, energy shifts, absorption, and meteorological and oceanographic circulation will degrade much of the incoming solar exergy. [...] Life is simply another means of destroying solar exergy.”

Life is, then, an extremely dissipative phenomenon that, by having the capacity to reproduce, is defined by the way it achieves the necessary compromise between satisfying the urge to explore all the possibly available exergy while also maintaining itself. From the different ways organisms perform this compromise and the spatial and hierarchical relation they have to one another, ecological structure is formed.

This general description of life fits quite nicely into some recent developments in non-equilibrium thermodynamics, particularly so for dissipative structures. These entities are characterized by being so far pushed out of equilibrium by their inputs that they develop ways to incrementally re-establish equilibrium. For example, the transition from laminar to turbulent flow or the development of convection in simple fluid thermal transfers are just two examples of such behaviour.

These paths to dissipation are typically structural, as in the case of the above mentioned phenomena, once they use the available energy entering the system for developing structures that are progressively more efficient at dissipating energy. In order to maintain their structure, these dissipative structures export the entropy they produce from the system, effectively generating negative entropy for themselves, by using the exergy imported from their surroundings (Prigogine and Stengers, 1984). In this way, they can maintain themselves and keep on destroying exergy. This formal framing can be used to analyse biological and ecological systems (Toussaint and Schneider, 1998). It becomes clear that, if left to itself and as a world-scale dissipative phenomenon, life tends to increase its own capacity for destruction of available exergy.

## 2.2 Ecological systems

Biological and ecological systems share their physical and phenomenological basis, consisting in similar energy and mass fluxes organized in order to maintain themselves and pursue their energy dissipating functions. This formal framework can be extended into other fields of science. For example, such reasoning can be applied to economic systems; in fact, similar analyses are already being made for this particular application (Sciubba and Ulgiati, 2005). However, these physical principles alone are not enough to completely characterize the behaviour of any system, although they provide the general fundamental rules; instead, specific principles must emerge at the respective level of scale and complexity to define its behaviour (Allen and Hoekstra, 1992).

Ecological systems represent the complex interaction between diverse biological systems and their surroundings. This not only encompasses their trophic inter-relationships but also the relative structure of their populations in terms of development and occupation of ecological niches. The knowledge of these systems is a natural extension of biology, as the population dynamics of every species depends on its fitness, ecological situation, inter-species connections and surroundings.

There are some basic units for ecological analysis, the most popular of which are organism, population, community, ecosystem, landscape and biome (Allen and Hoekstra, 1992). The distinguished levels of ecological structure are not based in spatial criteria but instead on phenomenological criteria. In this way, the existence of apparently contradictory entities is possible, e.g., a low-scale gastric ecosystem inside a larger scale whale individual.

Notice that the ecosystem components may be as distinctive as the individual biochemical pathways in a cell, both in spatial boundaries and in the variety of entities interacting in the system. Throughout the structural differences that stand between one case and the other, ecology as a science usually focuses on the difference between the sum of the parts and the total. Therefore, the move to larger ecosystems is no more a simple summation than is the move to an individual organism from its cellular biochemistry. The way in which this descriptive nature is attained at lower level of complexity is not trivial at all.

Given the importance of stochastic processes and chaos for natural selection and evolution, the path travelled by life in its quest for exergy destruction is hardly determined solely by the impositions made by the fundamental processes taking place both at lower and at higher levels of complexity.

Taken from an historical approach, life presumably first concentrated on the most available sources of dependable energy, such as chemical and thermal gradients around hydrothermal vents, and wherever the pervasive solar energy met sufficient nutritional and stoichiometric needs. There are also some theories that postulate that life arose heterotrophically, given high concentrations of complex organic molecules made possible by the planet's

early volcanic activity and high temperatures (Deamer, 2008). Either way, there was a relatively large amount of energy available for chemical reactions that lead to biosynthesis and organization.

Then, probably as a result of the diminishing availability of energy or nutrients, these primal organisms developed a way to focus and store energy and matter in reserve organic material, expanding the periods of time where they could go without direct sustenance (Kooi and Troost, 2006). This, while in apparent contradiction with the thermodynamic mission to destroy all the exergy they could, allowed certain organisms to outlast scarcity and to improve their exergy consuming capabilities across time. The popularity rise of energetic reserves also led to the accidental by-product of trophic chains: heterotrophic organisms began consistently using other organisms for nutritional purposes instead of producing their own sustenance directly by harnessing available energy.

The usual biological growth plan of brute force that leads to exponential growth encounters strong challenges when, by itself or in aggregation with competing entities, the organism reaches its environment's limitations. In this conditions, the plan mutates from exponential expansion, where the fastest grower thrives, to carrying capacity regulated, slowly-but-surely establishment. It is in face of this adaptation that cycles arise as the solution for shortage and depletion. Without cycles, the system would quickly run out of resources and be subject to strong environmental constraints (Allen and Hoekstra, 1992). However, recycling induces higher energetic costs; the system has to take care of itself instead of growing fast and exhausting resources.

With the development of larger, more complex ecosystems and competition arenas, these constraints got stricter and led to another response to scarcity: diversification (Schuler, 2001). With specialisation, biological species narrow their ecological niches, allowing for more ecological space for other species.

Notice that these strategic upgradings may have not been so clearly sequenced as the text might lead to believe, having intermingled throughout history and wherever an ecological succession is taking place, but the point remains: when constrained, whatever the scale may be, life develops ways to keep on destroying exergy, most of the times at the expense of the short-term.

This holistic upscaling of dissipative structures achieves its peak with the presentation of the Gaia hypothesis by Lovelock (1965). This approach conceptualizes the whole of planet Earth, with all its geological, atmospherical, biological and ecological dynamics, as a single inter-connected functioning system. Although being an interesting point of view, the practical value of this hypothesis does not go far beyond its illustrative properties. In order to use allow for more operational descriptions, the ecosystem is usually separated from the rest of the planet at a certainly arbitrary but ultimately needed boundary.

Hence, mature ecological systems tend to maintain themselves through careful management of resources and fluxes, whereas their biological components may often behave in a very unrestricted way. However, like their components, ecosystems are thermodynamic systems that continually maintain themselves out of equilibrium states (Kay and Fraser, 2002), reproducing the dissipative structure pattern to a higher level.

This analogy can be broadened into their systemic distinctiveness: as a whole, ecosystems can behave as a cohesive unit that pursues self maintenance and the usual dissipative goal of exergy destruction, in a way that can be analysed from a thermodynamic basis much as the organism can. In fact, the conceptualization of ecosystems as metabolic units, within which fluxes are managed and used by biologic life, is a strong area for development in what has been named “metabolic ecology” (Marquet et al., 2004).

While the organism is defined as a single, undividable biological system that functions independently, the ecosystem could be interpreted as an assembly of individual biological systems, or organisms, and their respective biological, atmospherical, and geological spheres of influence. In this way, the ecosystem comes to be an undividable ecological system in the sense that it encompasses all its components need to function independently. Hence, beyond the properties it has for being an aggregation of undividable functional systems, a given ecosystem also shares with them some analogous properties by being itself an independently functional system.

However, given the spatial and temporal scale and multitude of contributing factors, as well as their open nature, ecosystem behaviour tends to describe chaotic tendencies (Fath et al., 2001). As such, the theoretical approach to it comes from holistic, fuzzily defined goal functions instead of the relatively cleaner and precisely defined behaviours of lower complexity entities.

### **2.2.1 Ecological goal functions**

Ecological goal functions are the fuzzy behaviour orientators of ecosystem behaviour. These orientators are, as argued, motivated by growth and self maintenance, given the competitive environment ecosystems are subject to (Allen and Hoekstra, 1992). This competition has necessary roots in mass and energy availability, and as such with fundamental thermodynamics.

**The principles** There have been numerous attempts to join thermodynamic formalism with profound descriptions of ecosystems. In a recent attempt to generate a common theoretical basis, Jørgensen and Fath (2004) presented eight phenomenological principles or stylized facts as follow, abridged.

1. All ecosystems are open systems embedded in an environment from which they receive and discharge energy and matter.
2. Ecosystems have many levels of organisation and operate hierarchically.
3. Carbon-based life has a viability domain between about 250 - 350 K.
4. Mass and energy are conserved.
5. Life on earth has a shared basic biochemistry.
6. No organism exists in isolation but is connected to others.
7. All ecosystem processes are globally irreversible.
8. Biological processes use captured energy to move further from thermodynamic equilibrium and maintain a state of low entropy relative to its surroundings.

Although most of the principles presented are of general acceptance, the eighth principle is a relatively new development made to attempt explanation of many ecological observations. With it, the authors attempt to provide the presumably last formal piece needed to describe the macroscopical behaviour of ecosystems.

Notice that a similar principle could be stated about the behaviour of individual organisms; indeed, this reasoning is related to the general concept of dissipative structure.

**The types of growth** With larger distances to its thermodynamic equilibrium, measured in available energy or exergy, an ecosystem becomes more mature. Accordingly, ecological maturity, is achieved by a mixture of all the following four types of growth (Fath et al., 2004):

- 0 Boundary growth, that creates boundaries and permits inputs into the system;
1. Structural growth, when the physical scale of the system's components increases;
2. Network growth, when energy-matter transactions and pathways proliferate, increasing energy and nutrient cycling;
3. Information growth, when the system's behaviour changes from exploitative patterns to more conservative patterns, becoming more efficient and complex.

Although there is a typical temporal order in these types of growth, they can be simultaneously in progress and in whatever order happens to be more fit according to the environmental conditions. That being said, boundary growth has to take precedence, given that, by definition, there has to be a boundary across which to exchange inputs and outputs; thus the zero-th status.



**The behaviour orientators** Why healthy ecosystems tend to develop into more complex forms is a question that has been profusely asked. In a recent work Fath et al. (2004) present a group of hypotheses that presumably synthesize the most satisfactory goals for ecosystem growth and development, as follow:

1. Specific production of entropy tends to a minimum, as obtained by Prigogine and Stengers (1984) for systems distant but close to thermodynamic equilibrium.
2. Energy throughflow tends to a maximum within system limits, as discussed by Odum (1983) and Lotka (1922), as the ecosystem grows to use available inputs.
3. Exergy dissipation tends to a maximum, from the work of Schneider and Kay (1994), either indirectly by storage or directly with maintenance.
4. Ecological exergy tends to a maximum, as obtained by Jørgensen et al. (1995), especially when informational aspects are considered.
5. Retention time tends to a maximum by the increasing of scale for cycles and the meandering of pathways.

According to the results presented in the referred work, while all five are empirically validated at least in certain growth phases, only hypotheses 2 and 4 are consistently verified throughout the modelled ecosystem's evolution (Fath et al., 2004). Hence, energy throughflow and ecological exergy maximisations can be taken to determine a given ecosystem's maturity state. Consequently, ecological phenomena compete to become larger, more diverse, and better at dissipation.

In this way, ecosystems develop informational and structural quantity and variability, effectively moving away from thermodynamic equilibrium. This investment is highly nonlinear: an increase in genetic variability is presumably connected with an increase in biodiversity which leads to more ecological space being available, therefore compounding complexities at different levels and increasing the system's total ecological exergy.

Another line of inquiry has led to the conceptual connection of a given ecosystem's activity to its surface temperature, given that it controls major energy flux outputs. Hence, if an ecosystem tends to "maximize the available exergy, it can do so by controlling its surface temperature" (Kay and Fraser, 2002). With lower surface temperatures, the ecosystem can export more entropy-rich outputs in the form of longer wavelength radiation, allowing for higher specific entropy production in steady state, which raises the dissipative limits to the ecosystem. It is then expected that more mature natural ecosystems present lower surface temperatures than their younger, man-made counterparts, which is concordant with reported results (Luvall and Holbo, 1991; Akbari, 1995). Hence, with some measure of exergy inputs

and outputs of a given ecosystem, one could characterize how mature and how far from thermodynamic equilibrium the thermodynamic system is (Kay and Fraser, 2002). Notice that this type of analysis does not contradict the limitations identified earlier, in page 3, to system entropy production quantification. In fact, this method can only determine an upper bound for the dissipation promoted by the system.

The concept of emergy was derived by Odum in order to also account for quality needs in the context of energy throughflow assessment; empower is also a very important concept in ecosystem maturity and development analysis, in accordance to hypothesis 2. Some, like Bastianoni et al. (2006) go as far as to use the ratio of ecological exergy to empower as an index of the efficiency of an ecosystem usage of high quality inputs (in the form of high exergy content) for growth and development. This ratio represents the amount of available energy created in the ecosystem per flux of embodied energy in the inputs.

Based on the assumption that both empower and ecological exergy increase with the ecosystem's development, the ratio itself tends to a maximum (Bastianoni et al., 2006): as the population increases, supported by the presence of available inputs, empower increases. Then, existing communities adapt to the environmental restrictions as they become more relevant, maximizing ecological structure and, thus, increasing ecological exergy. Consequently, higher ecological exergy to empower ratios denote more efficient ecosystems, therefore further away from equilibrium.

Application of these ecosystem orientators is already taking place in several settings, particularly in eutrophicated bodies of water (Fonseca et al., 2002; Austoni et al., 2001), that are more easily controlled and measurable.

Some caution as to whether the particular formulation of ecological exergy, referred in page 6, is or not representative of the complexity imbued in the development of a given ecosystem must be taken. However, it is indisputable that varying levels of complexity exist in ecosystems and that higher levels of complexity (higher system exergy, if informational aspects are taken into account) lead to higher exergy consumption. "As ecosystems develop or mature they should therefore develop more complex structures and processes with greater diversity, more cycling, and more hierarchical levels all to abet exergy destruction" (Kay and Fraser, 2002).

In a way, ecosystems are both composed of dissipative structures and mechanistically similar to their component systems, which originates interesting analogies between ecology and biology but also a wide range of possible ambiguities. These ambiguities, allied with the fuzzy macroscopical behaviour of ecosystems, makes for a very difficult characterisation of fluxes and internal processes in a theoretically representative manner. Hence, this work's applications will focus primarily on the individual organism scale.

## 2.3 Biological systems

As already seen, life is a self-structuring and self-reproducing process in constant adaptation via evolutionary processes and in compliance with the fundamental laws of thermodynamics, and as so biological systems have deep connections with the availability of energy and associated mass fluxes.

The use of a given set of materials in energy transport and biosynthesis, the construction of biological components, introduces generalisable stoichiometric constraints to the metabolism. In a generic way, metabolism can be defined as the set of physical and chemical processes needed to maintain organisation and structure. This concept describes the transformations occurring inside and the fluxes demanded by and expunged from a cell, an organism or, at higher scale, a population such as an ant colony. However, full knowledge of a given metabolism can become quite extensive and unpractical. Hence, some aggregated measures are usually taken to represent metabolic functioning, such as dioxygen uptake rate or dissipated heat flux.

Another useful application of these aggregated measures is the way they scale across organisms, either in the same species, across related species or even across the whole spectrum of biological systems. These scaling regularities can be explored in relevant, explanatory applications but are usually only taken to be self-evident from statistical fits over limited experimental data values.

The approach to this type of system is somewhat different from the one presented for ecological systems, given the differences in the availability of theoretical descriptions in the literature. Hence, a formal framework is used to describe energy conversion and entropy production in biological systems, instead of resorting to more holistically defined analysis tools.

### 2.3.1 Quantification and quality

The problem of metabolic rate measurement is one of the most deep and recurrent questions in biology, given the variety of scales, types of metabolism and diversity of associated mass fluxes. How can a deep sea chemolithoautotroph with a strong hankering for sulphur be compared to a dioxygen using plankton sweeper whale from an energy point of view?

There have been two major aggregative answers to this question, each one with its own vulnerabilities: either quantify metabolic rate as proportional to a) a certain mass flux, usually dioxygen, misrepresenting those species that do not use it, like anaerobic bacteria, or b) released heat from the organism's surface measured by direct calorimetry.

DEB theory presents another approach with relatively disaggregated energy fluxes, such as energy rates allocated to growth or maintenance, that only depend on specific parameters

and state variables. These parameters also have to be obtainable indirectly from statistical data, but gain mechanistical relevance within the theoretical structure that supports them.

Aggregate measures, such as dioxygen consumption rate, are relevant if they are adequate. In certain cases, mechanistically accurate energy fluxes may be more useful. These disaggregated variables can then be used through conservation laws and stoichiometry to obtain any aggregated measure deemed necessary. In this work, we obtain both the dioxygen consumption flux and the dissipated heat flux, additionally proposing another aggregated quantificator of metabolic activity with entropy production. Paragraph (Text about why entropy production rules later)

Although the perfect solution would be to map out the full spectrum of biochemical compounds existent in any given cell of any given organism, such a task is beyond any measure of feasibility. Even if it wasn't, full knowledge of the used compounds would not necessarily lead to full knowledge about the system itself; knowledge about the mechanisms themselves would be essential to understanding the system. The same explanation could be given, as an example, for the reasons why ecology cannot be fully described only as an implicit function of its components' biochemistry. Although component behaviour is important, system dynamics are majorly affected by larger scale mechanisms, in such a way that different low-scale system details can originate similar high-scale system mechanisms. Only a truly representative measure could be used to compare across all types and scales of systems, even if one only considers biological systems. Hence, entropy production was chosen to represent biochemical activity because, given the theoretical background provided earlier, it represents a measure of the dissipative effects of the system being measured.

### 2.3.2 Allometry

Some statistical coherences of the distribution of general measurements according to body mass  $M$  have led to the use of allometric relations, where the variable  $Y$  is assumed to follow  $Y = Y_0 M^\alpha$ , with  $Y_0$  being a normalisation constant and  $\alpha$  the allometric exponent (Schmidt-Nielsen, 1984). Throughout the literature some relations are presented that fit data from across several orders of magnitude. This statistical fit approach to measured data is applied to many variables, being the most relevant the metabolic rate, usually represented by the dioxygen consumption flux, while other measures like time spans, rates and representative lengths are also found in the literature. Amongst others, Schmidt-Nielsen (1984) and Calder (1983) compiled and presented several sources for this type of data. In a more recent forum, Savage et al. (2004) compiled several sources of metabolic data.

Usually, metabolic rates scale with an exponent of  $3/4$  (Kleiber, 1932; Savage et al., 2004; West et al., 2002; Banavar et al., 2002), although values between  $2/3$  and 1 have also been found to fit available data (Dodds et al., 2001; White and Seymour, 2003; Labra et al.,

2007; Sibly and Brown, 2007; Makarieva et al., 2008). This variation is commonly associated with different classes of species and with their varying sizes (da Silva et al., 2006). Similarly, metabolic rates vary between resting and stressed situations, originating two different extreme applications: while the basal metabolic rate (BMR) is measured for resting conditions, the maximum metabolic rate (MMR) is measure in stress situations. These rates reportedly scale differently with body mass, with the BMR being approximated by a 0.75 power rule while the MMR can, for certain species, be approximated by as high as a 0.88 power rule (Bishop, 1999). Alternatively, both dissipated heat flux West and Brown (2005) and entropy production rate Andresen et al. (2002) are argued to scale similarly to the dioxygen flux.

Biological time scaling can be applied to any representative time lapse in an organism's existence, be it related to intracellular biochemistry, lifespan, heartbeat rate, respiratory rate, or any other lapse or rate that may be significant when different individuals or species are compared. Various authors have pursued statistical distributions for time lapses in biologic systems, usually mammals: Stahl (1967) presents heartbeat frequency and respiratory frequency for mammals, Lasiewsk and Calder (1971) for birds.

Although they can be statistically fitting, these relations do not necessarily provide any phenomenological explanation of the processes described. These rules have some fundamental problems relating to the involved variables and parameters that reflect their more profound lack of theoretical background.

Dimensional inconsistencies are inevitable when dealing with the normalisation constants (Kooijman, 2008). These constants have no physical or mechanistical meaning, given that they are obtained *a posteriori* and do not have a consistent dimension set; for example, the dimensions of any given metabolic rate normalisation constant would be  $\mathcal{E}.M^\alpha.t^{-1}$ . Also, given their empirical nature, these constants are prone to representativeness limitations given certain data specificities such as used species, experimental conditions and processes of measurement.

Such variability in statistical conditions further complicate the dimensionality analysis of the normalisation constants. Particularly, consider the case of consolidating multiple species values, in comparison to consolidating and fitting separately each species. These values would generally yield different approximations with different allometric exponents, that concurrently lead to normalisation constants that are different in value and, most importantly, in dimensions, in comparison to the globally obtained fit parameters.

Several attempts have been made to explain these power rules in depth. In association with the Metabolic Theory of Ecology (MTE), brought forth by Brown et al. (2004), the usual explanation involves the existence of a infinitely fractal hierarchical branching geometric network modelled to obtain the expected relation between body mass and metabolic rate, assuming that energy expenditure in transport is minimized and that the terminal branches are invariant (West and Brown, 2005). This explanation is similar to constructal theory,

by Bejan (2000); Reis and Bejan (2006); Bejan (2006), that is based on a minimization of transport costs in a finitely fractally-branching space-filling closed flow network with invariant terminal branches and conserved cross-sectional area.

However, there are some problems with this explanation. Only a very small fraction of organisms have a closed circulatory system, and the conservation of cross-sectional area implies that total flow in the aorta is the same as in the capillaries, while in reality it differs by several orders of magnitude. Even for the organisms that do have differentiated circulatory systems, there might be some limitations to the applicability of the MTE's basic assumptions (Kozłowski and Konarzewski, 2004). In a recent work, van der Meer (2006) exposed some of the inconsistencies of this theory in direct comparison to DEB theory. One of the most relevant is the fact that, dimensionally, any exponent's base has to be adimensionized. Hence, instead of  $M^\alpha$ , variables such as dioxygen consumption flux should be proportional to  $\left(\frac{M}{M_0}\right)^\alpha$ , introducing a third statistical parameter for the power law regression.

Similar explanations are based, in a simpler fashion, in the four dimensionality of the space in which the organism exists. This explanation, provided by da Silva et al. (2007), is based in four-dimensional energy and mass densities, assumed independent of body mass, that are manipulated into yielding the most common allometric exponents according to the dimensional constraints of the analysed system. By assuming constant densities this explanation imposes its inevitable outcome, without reference as to whether these assumptions are realistic or not or even the concept of four dimensional concentration itself.

A similar method led Feldman (1995) to the result that the value of the statistically derived exponent is dependant not only on the physical dimensions of the process but also on the biological characteristics of the system.

Another more developed approach to allometry includes multiple process rate limitation as a way to incorporate the differences between BMR and MMR. Darveau et al. (2002) present a model that complements the concept of metabolic rate with its contributing steps, such as dioxygen flux or cellular supply pathways. The exponent obtainable from a regression of the metabolic rate, in this model, can be achieved as a weighted sum of the exponents of its contributing steps, as seen in equation 3.

$$B = B_0 \sum c_i M^{b_i}, \quad (3)$$

where  $B$  is metabolic rate,  $B_0$  is the normalisation obtainable from the aggregated fit,  $c_i$  are the constants obtainable from separate regressions done for differently limiting steps, and  $i$  is a given contributing step. With this model, differences in regimes of stress are then explainable as varying values for the regression constants, which symbolize different weights for the contributing factors of the metabolic rate.

From the concept of specific metabolic rate, dimensioned as  $\mathcal{E}.M^{-1}.t^{-1}$ , one can obtain

the reciprocal metabolic time. However, this is generally done without concern for dimensional correctness: it is commonly argued in the literature that the specific metabolic rate has dimensions of  $t^{-1}$ , once the massic consumption of dioxygen cancels dimensionally with the biological mass, originating a surrogate reciprocal metabolic time. However, the true dimensions of the specific metabolic rate are  $\mathcal{E}.M^{-1}.t^{-1}$ , which only correspond neatly to  $t^{-1}$  if there is a clear relation between metabolic power and a related mass flux, normally dioxygen.

The consequences of this imprecision may vary from irrelevant, when the organism practices a well-behaved heterotrophic metabolism, to profoundly incorrect, in the case of autotrophs or organisms that don't consume dioxygen in a way directly correlated with their use of energy.

Additionally, there is some confusion about metabolic or dioxygen rate and their respective implications for entropy production, especially since dioxygen is expected to play some role in biochemical aging. There is no reason to believe that entropy production behaves in the same way as the metabolic power rate with dioxygen consumption throughout all organisms (Sousa et al., 2006). In fact, although entropy production has a close connection with energy transformation, it does not have to be strictly proportional. It can, however, be used as a measure of metabolic activity.

This means that, although biological time scales may be associated with specific entropy production (Andresen et al., 2002), neither is necessarily connected to dioxygen consumption in the same way for every type of organism or metabolism.

In this light, some recent results obtained by Andresen et al. (2002) should be questioned, once they are based in the reciprocity between the power laws of specific metabolic rate and metabolic time and also on the direct relationship between metabolic rate and entropy production. These authors establish a set of necessary conditions for minimal entropy production in biological systems, using a general non-equilibrium thermodynamics result that limits maximum efficiency to systems that produce entropy at constant rates in their intrinsic time scale.

In a related work, Andresen and Gordon (1994) showed that the general necessary condition for minimum entropy production is a constant rate of entropy production on the intrinsic time scale. By connecting biological time lapses with physiological intrinsic time, the authors trace the physical perception of passing time to thermodynamic speed and to the internal production of entropy.

From the general applicability of the allometric rules to metabolic rate, in particular to entropy production rate, and physiological time, Andresen et al. (2002) obtain that biological systems are all equally efficient. Additionally, given that these assumptions result in constant entropy production in the physiological time, these authors obtain that biological systems verify at least one condition to be maximally efficient, to have a constant entropy production

rate (Spirkl and Ries, 1995). With the initial assumption that entropy production can only be directly associated to metabolic rate in isothermal processes, the authors then infer that in these cases entropy production rate scales with  $M^{3/4}$ , just like any other relevant rate. By defining physiological time as a well-behaved  $t = t_0 M^{1/4}$ , total entropy production in a certain physiological time is then proportional to  $M$ . From here, the conclusion that total entropy production per unit body mass in respective intrinsic time should be the same for all species is obtained. This would mean that all metabolisms would be equally irreversible in their own time scales.

However, both basic assumptions have inconsistencies. In this section of the work, a surrogate physiological time rate for the DEB organism will be defined in order to examine such hypotheses.



### 3 Dynamic Energy Budget theory

This chapter describes the used DEB model and its internal functioning. In section 3.1 the set of general assumptions and schematics is laid down, while section 3.2 describes in further detail the used formal description of an individual organism's metabolism.

#### 3.1 General description

DEB theory, put forth by Kooijman (2000), lays theoretical and formalistic foundations for the mechanistic description of biological processes. This theory predicts and explains a certain set of stylized facts, presented in Table 1, summarized in a posterior formalisation of the theory (Sousa et al., 2008).

This theory is based in the abstraction of a given organism as separable, constant composition units of structure,  $V$ , and reserve,  $E$ , that represent structural volume and reserve energy, respectively. These state variables represent two groups of compounds that perform different functions for the organism. The most fundamental difference between these state variables, aside from dimensional considerations, is that while structure compounds have maintenance costs inherently associated, reserve compounds have no maintenance; this can be argued to be resultant from their low retention time. For instance, while structure represents biologically active compounds, that are built upon, maintained, and eventually substituted, reserve represents compounds used for energy transport and production, that are naturally used up at higher rates. Notice that this does not mean that they represent different chemical compounds, once the same molecule can play both roles in its lifespan.

Table 1: Stylized facts explained by DEB theory.

Feeding	<p>Starving organisms may reproduce</p> <p>Starving organisms may grow</p> <p>Starving organisms survive for some time</p>
Growth	<p>The growth of isomorphic organisms at abundant food is well described by von Bertalanffy growth curve (von Bertalanffy, 1938)</p> <p>Many species do not stop growing after reproduction starts</p> <p>Foetuses increase in weight proportional to cubed time</p> <p>The logarithm of the von Bertalanffy growth rate of different species corrected for a common body temperature decreases almost linearly with the logarithm of the species' maximum size</p> <p>The logarithm of the von Bertalanffy growth rate for organisms of the same species at different food availabilities decreases linearly with ultimate length</p> <p>Egg size covaries with the nutritional status of the mother</p>
Respiration	<p>Freshly laid eggs do not use dioxygen in significant amounts</p> <p>Dioxygen consumption increases with decreasing mass in embryos and increases with mass in juveniles and adults</p> <p>The use of dioxygen scales approximately with body weight raised to power 0.75 (Kleiber, 1932)</p> <p>Organisms show a transient increase in metabolic rate independent of their body mass after ingesting food</p>
Stoichiometry	<p>Well-fed organisms have a different body chemical composition than poorly fed organisms</p> <p>Organisms growing with constant food density converge to a constant chemical composition</p>
Energy Dissipation	<p>Dissipating heat is a weighted sum of three mass flows: carbon dioxide, dioxygen and nitrogenous waste</p>
Cells	<p>Cells in a tissue are metabolically very similar, independently of the size of the organisms</p>

Another basic assumption of this theory is that, given a constant level of feeding, the organism's composition, and therefore its ratio between components  $E$  and  $V$ , tends to a constant value. These and other assumptions for the standard DEB model were obtained in a discussion of concepts by Kooijman (2001) and are presented in Table 2.

Table 2: Assumptions for full standard DEB model specification.

Mass and energy	<p>Structural body mass and reserves are the constant composition state variables of the individual</p> <p>Food is converted into faeces, and energy assimilated from food is added to reserves. Reserves fuel all other metabolic processes, classifiable into three categories: synthesis of structural body mass, synthesis of gametes, and processes not associated with synthesis</p> <p>If the individual propagates via reproduction, it starts in the embryonic stage, and initially has a negligibly small structural mass</p> <p>The reserve density of the hatchling equals that of the mother at egg formation. Foetuses develop as embryos in eggs, but at a rate unrestricted by energy reserves</p>
Powers	<p>The transition from embryo to juvenile initiates feeding; that from juvenile to adult initiates reproduction, with cessation of maturation</p> <p>These transitions occur when cumulated energy invested in maturation exceeds certain values</p> <p>Somatic and maturity maintenance are proportional to structural body volume, but maturity maintenance doesn't increase after a given cumulated investment in maturation. Heating costs for endotherms are proportional to surface area</p> <p>The feeding rate is proportional to the surface area of the organism; the food handling time and the digestion efficiency are independent of food density</p> <p>The reserves must be partitionable, such that the dynamics are not affected; the reserve density at steady state does not depend on structural body mass</p> <p>A fixed fraction of energy, used from the reserves, is spent on maintenance plus growth, the rest on maturity maintenance plus maturation or reproduction</p> <p>under starvation, individuals always give priority to somatic maintenance and either do not change the reserve dynamics, continuing investment in or reproduction, or cease investment, changing reserves dynamics</p>
Ageing	<p>Dioxygen causes net DNA damage with a certain efficiency</p> <p>Damaged DNA produces 'wrong' proteins at a constant hazard rate, which accumulate in the body</p> <p>Hazard rate is proportional to the density of 'wrong' proteins</p>

Further detailed explanations of the theory can be obtained in related literature (Kooijman, 2000; Sousa et al., 2008; Nisbet et al., 2000). Adequate theoretical treatment of biological metabolism is essential to explain why and how the systems develop in the way they do and what are the consequences. This DEB theory-based treatment can be partic-

ularized, with further model extensions and parameter values, for specific implementations, such as algae, plants or more complex organisms, allowing sound mechanistical explanations for empirical facts. For example, Darwinian evolution is modeled in DEB theory by introducing random variations for the parameter values Kooijman (2009).

### 3.1.1 Metabolic schematics

The metabolic rate is a rather intangible variable; usually, some sort of proportionality with dioxygen uptake is assumed, which is necessarily only true for aerobic organisms. Nonetheless, DEB theory accommodates a degree of analysis that can potentially avert these generalisations, by particularizing different energy fluxes inside the organism. This particularisation is presented in Figure 1, where oval boxes represent state variables and rectangular boxes represent processes.

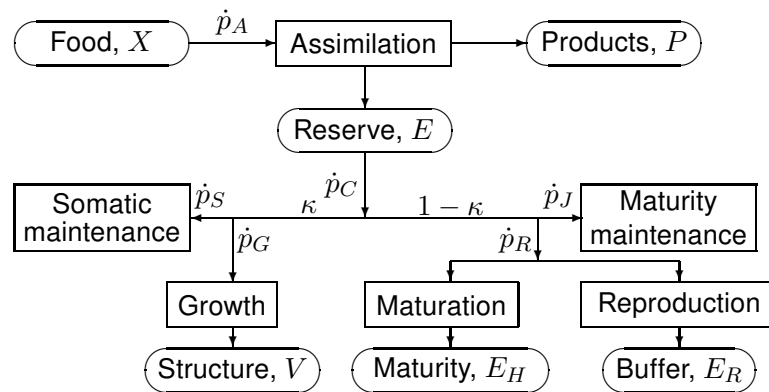


Figure 1: Metabolic allocation schematics

Available energy enters the reserves by the assimilation of food, represented by  $\dot{p}_A$ . Reserves fuel all metabolic processes according to the mobilized catabolic power flow  $\dot{p}_C$ , being a constant  $\kappa$  fraction of it allocated to somatic maintenance  $\dot{p}_S$  and growth  $\dot{p}_G$  and the remaining  $1 - \kappa$  fraction allocated to maturity maintenance  $\dot{p}_J$  and  $\dot{p}_R$ , that corresponds to maturity development in earlier life stages and to reproduction in adulthood. Somatic maintenance refers to expenses in cellular stabilisation, protection and chemical control, while maturity maintenance is associated with cellular differentiation. Allocation to somatic (maturity) maintenance takes precedence over growth (maturation or reproduction). Nevertheless, certain model extensions can be made in order to contemplate investment-motivated shrinkage, once available energy may not be enough to account for and all maintenances.

Notice that there is a bifurcation on the maturity and reproduction side of the scheme. This is because such processes take place at different life stages: while investment in

maturation is made during the embryo and the juvenile stages, investment in reproduction only takes place during adulthood. These investments have necessarily different purposes. While maturity development allocates energy that is completely dissipated by producing organisational structure that represents a purely informational investment in the DEB variable maturity, identified as  $E_H$ , reproduction energy allocation accumulates reserve in a buffer  $E_R$  that is periodically released into the environment in the form of offspring.

Maturity  $E_H$  is the prime variable for the establishment of threshold values for life stage transitions; however, these investment thresholds can be replaced by other, simpler, length conditions, if both maintenance rate coefficients are equal, i.e.,  $\dot{k}_M = \dot{k}_J$ . These maintenance rate coefficients are defined as

$$\dot{k}_M = \frac{\dot{p}_M}{E_G}, \quad \dot{k}_J = \frac{\dot{p}_J}{E_H}, \quad (4)$$

where  $E_G$  represents the energy costs of new structure, obtained as  $V \times [E_G]$ , where  $[E_G]$  is the constant volume-specific costs of new structure, defined later in table 3.

These length threshold conditions are generally satisfactory for birth transitions (Kooijman, 2009), given the relatively stable development conditions for embryos. However, puberty is a more subtle case, because organisms are subject to extreme instability in feeding, even in experimental conditions. Additionally and perhaps consequently, the biochemical and cellular changes that lead to puberty transitions are relatively uncharted territory (Kooijman, 2009), and as such there is no way to present another mechanism for this transition without making significant detours to the presented analysis. Hence, the approximated transition length condition is used, which in other words means that the equivalence of maintenance rates coefficients is assumed.

In DEB theory, an embryo's reserves are fully provenient from the mother's released reproduction buffer. This reserve is invested in growth and maturation, with the necessary increasing of both somatic and maturity maintenance. Once maturity, that in this model is assumed to be proportional to structure, reaches the birth threshold value, the embryo turns into a juvenile and starts assimilating, therefore obtaining its reserve from the transformation of food, while both investments persist.

With the next accumulated maturation investment threshold the organism enters adulthood, and therefore allocation to maturity stops and is directed towards reproduction and the reproduction buffer, that is periodically released into the environment in the form of offspring.

Notice that if the feeding conditions are constant throughout the organism's life-cycle, reserve density  $[E] = E/V$  tends to a constant value, therefore making structure the only true variable of the model.

Both structure and reserve can be scaled in order to yield adimensional quantities according to maximum values; this promotes flexibility in the use of state variables. Scaled structural length  $l$  is given by  $l = (V/V_m)^{1/3}$ , where maximum structural volume  $V_m$  is a compound parameter obtained as described in page 27. Scaled reserve density  $e$  is given by  $e = [E] / [E_m]$ , where maximum reserve density  $[E_m]$  is another compound parameter also defined in page 27.

### 3.2 Model description

The standard DEB model is then based in single reserve and structural volume dynamics. Although simple, this configuration is sufficiently accurate to describe all the assumptions presented in Table 2, relevant for most animals. As such, the standard DEB model will be used to pursue the presented objectives for a typical isomorph animal, with the use of one reserve, one structure with three life stages (embryo, juvenile and adult) description. Isomorphism is basically a description of the way the organism grows in terms of physical dimensions; with an increase in structural volume, surface area varies proportionally to  $V^{2/3}$ , given that the organism maintains its shape throughout its life-cycle. Other examples of morphism are V-0 morphs, that actually do not change physical volumes because they are constricted in fixed membranes, and V-1 morphs, that maintain one length approximately constant throughout their life cycle, such as cylindrical organisms.

The scaled lengths  $l_b$  and  $l_p$  stand for the ratio of length to maximum length at the two considered maturity stage transitions: birth and puberty. Birth marks the start of assimilation, corresponding to a transition between embryo and juvenile stages, while puberty marks the beginning of allocation to development and reproduction, corresponding to a transition from juvenile into an adult individual.

Additionally, thermal maintenance costs are considered null i.e., the organism is ectothermic, and scaled energy buffer allocated to reproduction  $e_R$  is negligible compared to scaled reserve density. Further parameter values, typical for animals (Kooijman, 2009), are displayed in Table 3.

Table 3: Parameter description for a 1-E, 1-V, 3-S isomorph in DEB.

Par	Description	Value	Units
$\{\dot{p}_{A_m}\}$	Max. spec. assimilation power rate	11.6	$\text{kJ.cm}^{-3}$
$\dot{v}$	Energy conductance	1.0	$\text{cm.d}^{-1}$
$\kappa$	Fraction of useful energy	0.8	–
$\kappa_R$	Fraction of useful reprod. energy	0.8	–
$[\dot{p}_M]$	Maximum energy density	0.68	$\text{kJ.cm}^{-3}$
$\{\dot{p}_T\}$	Surface-specific heating rate	0	$\text{kJ.d}^{-1}$
$\dot{k}_M = \dot{k}_J$	Maintenance rate coefficient	0.05	$\text{d}^{-1}$
$[E_G]$	Volume-specific cost of new structure	13.6	$\text{kJ.cm}^{-3}$
$l_b$	Scaled length at birth	0.125	–
$l_p$	Scaled length at puberty	0.80	–
$T$	Temperature	293	K
$\mu_E$	Reserve chemical potential	283.3	$\text{kJ.mol}^{-1}$
$e_R$	Scaled energy allocated to reprod.	0	–
$d_V$	Structure density	1.0	$\text{g.cm}^{-3}$
$y_{EX}$	Reserve to food coupler	0.75	$\text{mol.mol}^{-1}$
$y_{PX}$	Product to food coupler	0.20	$\text{mol.mol}^{-1}$
$y_{EV}$	Reserve to structure coupler	1.15	$\text{mol.mol}^{-1}$

Some of the presented values, such as the reserve chemical potential or the oxygen couplers, are obtained from compound stoichiometry and metabolic dynamics. Other values, such as  $e_R$ ,  $l_b$ ,  $l_p$ , and temperature are educated guesses, made in order to simplify the model without taking any of the relevant mechanisms away from the description. The remaining parameter values were gathered from the representative animal parameter set of *DEBtool*, the computational set of tools for direct application of DEB theory. On page 27, stoichiometric parameters are presented, such as macro-chemical composition of the simplified compounds considered.

Compound parameters can be devised to provide more elegant parameters and to allow direct comparison with empirically obtained usual growth parameters. The expressions for compound parameters are synthesised in Table 4.

Table 4: Compound parameters description.

Par.	Description	Expression	Units
$[E_m]$	Maximum reserve density	$\{\dot{p}_{A_m}\}/\dot{v}$	$\text{Jcm}^{-3}\text{d}^{-1}$
$g$	Investment ratio	$\frac{[E_G]}{\kappa[E_m]}$	–
$[\dot{p}_M]$	V. Specific structural maintenance costs	$\dot{k}_M [E_G]$	$\text{Jcm}^{-3}\text{d}^{-1}$
$L_m$	Maximum length	$\frac{\kappa\{\dot{p}_{A_m}\}}{[\dot{p}_M]}$	cm

From these compound parameters, maximum structural volume can be defined as

$$V_m = L_m^3 = \left( \frac{\kappa \{\dot{p}_{Am}\}}{[\dot{p}_M]} \right)^3. \quad (5)$$

Although the starting point for DEB theory is the organism's life-cycle, it also allows for inter-species comparisons, especially for the comparison of related species, defined as species that deviate in their parameter values from each other in a very special way: certain parameters remain constant, once they characterize internal cellular processes, while others, affected by the scale of the organism, vary accordingly to changes in maximum volume, in particular proportionally to maximum length. The first are named constant primary parameters, while the second are named design primary parameters. Table 5 organizes most parameters according to spatial nature.

Table 5: Parameter conversions for a reference species.

Constant primary parameters		Design primary parameters
$[E_G]$	$\eta_{*1*2}$	$V_m^{1/3}$
$\dot{v}$	$\kappa$	$V_b^{1/3}$
$[\dot{p}_M]$	$\mu_E$	$V_p^{1/3}$
$\{\dot{p}_T\}$	$\dot{k}_M$	$\{\dot{p}_{Am}\}$

From this classification of parameters and with the additional conditions that the analysis is conducted for fully grown ( $l = 1$ ) individuals at equilibrium with access to abundant food ( $e = 1$ ), all DEB expressions can be converted into inter-species analysis tools. Necessarily, expressions that do not explicitly involve parameters, such as general balances, are directly applicable to an inter-species analysis, once the variables used in such equations are themselves converted for the inter-species analysis. In this way, while an intra-species analysis follows an individual organism's growth, an inter-species analysis compares fully grown adults of different species with different maximum sizes.

Although it is based on mechanistically stipulated variables with often small to none direct experimental measurability, DEB theory can use experimentally available variables such as wet weight. A very recent work by Kooijman et al. (2008) describes in a generisable way a practical guide to produce DEB theory parameters from data sets.



This model can be analysed in terms of mass fluxes, provided some assumptions about the different theoretical compounds' compositions are made. The following compositions and properties, presented in Table 6, are assumed to be representative of mineral ( $CO_2$ ,  $H_2O$ ,  $O_2$  and  $NH_3$ ) and organic (food  $X$ , structure  $V$ , reserve  $E$ , and products  $P$ ) fluxes for an animal that uses ammonia as the nitrogenous waste compound.

Table 6: Mineral and organic components' chemical composition, chemical potential, molar enthalpies and molar entropies.

Par.	$CO_2$	$H_2O$	$O_2$	$NH_3$	$X$	$V$	$E$	$P$	Units
#C	1	0	0	0	1.00	1.00	1.00	1.00	#.# <sup>-1</sup>
#H	0	2	0	3	1.80	1.80	2.00	1.80	#.# <sup>-1</sup>
#O	2	1	2	0	0.50	0.50	0.75	0.50	#.# <sup>-1</sup>
#N	0	0	0	1	0.20	0.15	0.20	0.15	#.# <sup>-1</sup>
$\bar{h}$	-393	-286	0	-80.1	-117	-107	-33	-117	$kJ.mol^{-1}$
$\bar{s}$	213.5	69.8	204.8	111.2	36.0	52.0	74.8	35.0	$J.K^{-1}.mol^{-1}$

Notice that all organic molar fluxes and indexes are reduced to a C-mol basis: instead of representing  $6.022 \times 10^{23}$  "whole" molecules, a C-mol represents all chemical indexes in proportion to an atom of carbon. As an illustrative example, if glucose was modelled, instead of accounting for a mol of  $C_6H_{12}O_6$ , the model would account for 6 C-mol of  $CH_2O$ . As could be seen with more complex examples such as the simplified compounds considered, this mode allows for neater calculations, even if at the expense of familiarity.

Entropy and enthalpy vectors for compound group  $*$  are respectively  $\bar{s}_*$  and  $\bar{h}_*$ , with  $*$  =  $\mathcal{M}$  for mineral compounds and  $*$  =  $\mathcal{O}$  for organic compounds. Formation enthalpy values of mineral compounds were taken from the *Handbook of Chemistry* Dean (1979) for mineral compounds. Formation enthalpy values for  $X$  and  $P$  were computed using Thornton's coefficient of  $-444$  kJ/mol of  $O_2$  and the entropies were computed using an empirical rule proposed by Battley Battley (1999). Formation enthalpies and entropies for  $E$  and  $V$  were obtained from a work by Sousa et al. (2006).

From the definition of the organism as two bulk substances, reserve and structure, the wet weight of the individual is obtainable as the sum of the respective contributions from each of these compounds

$$W_w = d_V V + \frac{w_E}{\mu_E} (E + E_R), \quad (6)$$

where  $d_V$  is the structure's density,  $w_E$  is the reserve's molar weight,  $\mu_E$  is the reserve's chemical potential, and  $E_R$  is the reproduction buffer and, according to the assumptions made in page 26,  $E_R \ll E$ .

Hence, wet weight for intra-species and inter-species are obtainable as, respectively,

$$W_w = \left( d_V + e [E_m] \frac{w_E}{\mu_E} \right) V \quad (7)$$

and

$$W_w^{(e)} = \left( d_V + \frac{L_m}{L_m^{REF}} [E_m] \frac{w_E^{1/3}}{\mu_E} \right) V_m \quad (8)$$

formally quantificating this variable as an explicit function of only structural volume and maximum structural volume respectively, according to the assumptions made about the organism.

### 3.2.1 Physiological time

Different systems, in particular biological systems, react to the environment they are immersed in with different speeds. Heart rates, respiratory rates, and most of the representative time lapses scale in a traceable way across organisms (Schmidt-Nielsen, 1984).

If representative, these scaling time lapses can be a proxy for the way the studied organism perceives passing time (Schmidt-Nielsen, 1997), hence meriting the title of physiological time lapse. In standard DEB theory, given the strong relevance given to energy issues, the reserve turnover rate will be used as a surrogate physiological time lapse.

As  $\dot{p}_C$  represents the mobilisation of energy from the reserve, the definition of the reserve residence time at a stationary state is straightforward as  $t_E = \frac{E}{\dot{p}_C}$ . This time lapse is a reasonable candidate for the role of physiological time lapse, once it conveys a certain notion of metabolic speed. As all metabolic activities derive their energy from the reserve, its residence time is significantly representative as a measure of metabolic activity.

The expression for the reserve residence time for inter-species analysis is obtained as

$$t_E^{(e)} = \frac{[E_m] V_m^{4/3}}{V_m^{REF,1/3}}. \quad (9)$$

The described model will be used to verify referred assumptions made in the literature about entropy production and physiological time.

### 3.2.2 Metabolic rates

In the formal structure of DEB some energy transfer rates are distinguished. Given the level of mechanistic disaggregation, there is no direct equivalent to a true metabolic rate in DEB theory, although  $\dot{p}_A$ ,  $\dot{p}_C$ ,  $\dot{p}_D$  or  $\dot{p}_{T+}$  can, each for its own reasons, be argued to be representative of the organism's energetic scale. All the following reasoning and expressions are specific for the used implementation of the DEB theory; however, similar considerations can be made for any other particular use.

Assimilation rate  $\dot{p}_A$  represents all free energy fixed into reserves from food uptake. By considering only the inward flux of energy, this rate avoids any considerations into what kind of dynamics or allocation strategies take place inside the organism. This variable is then representative of an organism's energy scale, but may not be sufficient to correlate with metabolic rate, once it is null for fasting individuals that continue their metabolic activity. Assimilation power rate  $\dot{p}_A$  aggregates all the uptake  $X + Minerals \rightarrow E + Minerals$  reactions that amount to cellular "income". This uptake is made proportionally to the organism's surface area, also being affected by food availability. The general definition of assimilation

rate is presented in equation 10.

$$\dot{p}_A = f\{\dot{p}_{A_m}\}V^{2/3}, \quad (10)$$

where  $f = X(X_K + X)^{-1}$  is defined as the functional response, in every way similar to the formulation of Michaelis-Menten kinetics, and  $\{\dot{p}_{A_m}\}$  is a design primary parameter quantifying the maximum surface-area-specific assimilation rate.

Catabolic mobilisation rate  $\dot{p}_C$  denotes energy obtained from the reserves for multiple uses, representing the amount of energy used by the organism. The general expression for this power is

$$\dot{p}_C = \dot{p}_S + \dot{p}_J + \dot{p}_G + \dot{p}_R. \quad (11)$$

This power rate then symbolizes all energetic “spending” done in the organism towards maintenance  $\dot{p}_S + \dot{p}_J$ , growth  $\dot{p}_G$  and reproduction or development  $\dot{p}_R$ . Growth rate  $\dot{p}_G$  has the particularity of accounting for all energy use in  $E + Minerals \rightarrow V + Minerals$  biosynthesising reactions.

The model expression for  $\dot{p}_C$  results from the reserve dynamics, given by  $\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$ . These dynamics are affected by a couple of basic assumptions in DEB theory mentioned earlier in pages 22 and 23, respectively: first, organisms growing with constant food density converge to a constant chemical composition, also known as the weak homeostasis assumption, and secondly the partitionability of reserve kinetics, that stipulates that the resulting reserve kinetics are not affected by separately considering any given set of reserves or the whole.

In a theoretical derivation that exceeds the level of complexity chosen for this description, Kooijman obtains the following expression for the catabolic mobilisation flux (Kooijman, 2009).

$$\dot{p}_C = E \frac{[E_G] \frac{\dot{v}}{V^{1/3}} + [\dot{p}_M]}{\kappa [E] + [E_G]}. \quad (12)$$

The maintenance power rates are simply proportional to some measure of size. Somatic maintenance is  $\dot{p}_S = [\dot{p}_M] V + \{\dot{p}_T\} V^{2/3}$ , which in an ectotherm corresponds to  $\dot{p}_S = [\dot{p}_M] V$ .

Maturity maintenance is proportional to the overall energy allocated to maturation, identified as  $E_H$ . However, given the simplificative assumptions made about maintenance length is also a good measure for maturity: with  $\dot{k}_M = \dot{k}_J$ , allocation to maintenance is proportional at both sides of the allocation scheme presented in page 24, which means that  $V$  and  $E_H$  grow proportionally in the earlier stages of the organism's life cycle. Consequently, maturity maintenance power rate is given by  $\dot{p}_J = \frac{1-\kappa}{\kappa} [\dot{p}_M] \min\{V, V_p\}$ .

Growth is defined as the increase in structural volume, and as such the power rate allocated to growth is obtained (Kooijman, 2009) as  $\dot{p}_G = [E_G] \frac{dV}{dt}$ , with

$$\frac{dV}{dt} = \frac{[E] \dot{v} \kappa V^{-1/3} + [\dot{p}_M]}{\kappa [E] + [E_G]} V. \quad (13)$$

Finally, energy allocated to maturation or reproduction  $\dot{p}_R$  is the  $1 - \kappa$  fraction of  $\dot{p}_C$  that is not needed for maturity maintenance, effectively being defined by

$$\dot{p}_R = (1 - \kappa) \dot{p}_C - \frac{1 - \kappa}{\kappa} [\dot{p}_M] \min\{V, V_p\}. \quad (14)$$

Dissipative power,  $\dot{p}_D$ , is

$$\dot{p}_D = \dot{p}_S + \dot{p}_J + (1 - \kappa_R) \dot{p}_R, \quad (15)$$

where  $\kappa_R$  is the efficiency of the maturation or reproduction process, being null for the phases when maturation takes place and close to 1 at adulthood. The value for  $\kappa_R$  is null for earlier life stages because the maturation process is conceptualized as a fully dissipative process: energy allocated to it is completely used up for the development of informational complexity.

This energy flux, by being used for purely internal reorganization and maintenance, leave no direct result other than changes in the informational state of the organism. As such, dissipative power accounts for all the most “purposefully wasted” energy used up in dissipative  $E + Minerals \rightarrow Minerals$  reactions.

This is, understandably, not the best proxy for metabolic power, once it does not consider growth investment and only indirectly connects to the existent structure via maintenance power. Notice that these reactions do not include the overhead costs of other processes, such as assimilation and growth; this was an arbitrary choice in the development of DEB theory (Kooijman, 2000).

However, in DEB theory, dissipative power plays a central role, constituting along with assimilative and growth powers the three fundamental macro-chemical reactions that fully specify the individual as a dynamic system (Kooijman, 2000), being generally referred to as  $\dot{\mathbf{p}} = \left[ \dot{p}_A \quad \dot{p}_D \quad \dot{p}_G \right]^T$ .

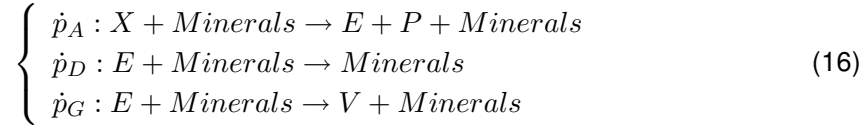
The used expressions for obtaining the power rates are presented in Table 7, according to the basic DEB theory (Kooijman, 2009), after division by a reference power rate equal to  $\{\dot{p}_{A_m}\}L_m^2 = [E_m]V_m\dot{k}_{MG}$ , that represents the maximum power rate available to the organism. In this way, all presented adimensionalized power rates have a value between 0 and 1.

Table 7: Power rate expressions for the modelled organism.

$\frac{\dot{p}_*}{\{\dot{p}_{A_m}\}L_m^2}$	Intra-species			Inter-species
	embryo	juvenile	adult	fully grown adult
$A$	0	$fl^2$	$fl^2$	1
$C$	$e l^2 \frac{g+l}{g+e}$	$e l^2 \frac{g+l}{g+e}$	$e l^2 \frac{g+l}{g+e}$	1
$S$	$\kappa l^3$	$\kappa l^3$	$\kappa l^3$	$\kappa$
$J$	$(1 - \kappa) l^3$	$(1 - \kappa) l^3$	$(1 - \kappa) l_p^3$	$(1 - \kappa) l_p^3$
$G$	$\kappa l^2 \frac{e-l}{1+e/g}$	$\kappa l^2 \frac{e-l}{1+e/g}$	$\kappa l^2 \frac{e-l}{1+e/g}$	0
$R$	$(1 - \kappa) l^2 \cdot$ $\cdot \frac{e-l}{1+e/g}$	$(1 - \kappa) l^2 \cdot$ $\cdot \frac{e-l}{1+e/g}$	$(1 - \kappa) \cdot$ $\cdot \left( l^2 \frac{e-l}{1+e/g} + l^3 - l_p^3 \right)$	$(1 - \kappa) \cdot$ $\cdot (1 - l_p^3)$

### 3.2.3 Mass fluxes, respiration and dissipated heat

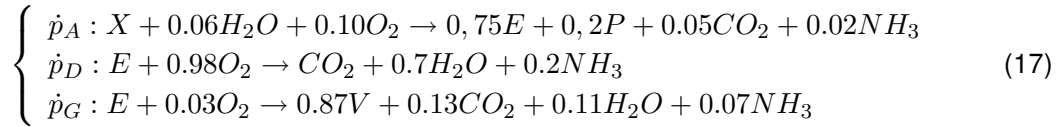
The vector  $\dot{p}$  is central to the mass and energy fluxes aspects of DEB theory, as a particular case of the freedom level restriction to any three fluxes that characterize the system, presented earlier in Table 1. These three fluxes have the particularity of separately grouping reserve produced in assimilation, reserve used in growth, and reserve used in dissipation. These fluxes are represented in equation 16.



As mentioned, the organism is fully specified as a dynamic system by these three fluxes, leading to the validation of the three degrees of freedom of indirect calorimetry Kooijman (2000). Fluxes such as the dioxygen flux, the dissipated heat flux or the entropy production rate are obtained as functions of parameters and these three rates.

In other words, the amounts of dioxygen, dissipated heat and entropy consumed or produced per aggregated chemical reaction can be obtained from mass, energy and entropy balances to each of these reactions.

The three stoichiometrically correct macro-chemical can be obtained by equating conservation of total number of chemical elements, yielding equation 17.



By considering the associated enthalpy content and the heat generated by each reaction, the respective contributions towards dissipated heat are obtained in equation 18.

$$\begin{cases} \dot{p}_A : q_{\dot{p}_{T^+,A}} = - \sum n_{i,A} \bar{h}_{i,A} \\ \dot{p}_D : q_{\dot{p}_{T^+,D}} = - \sum n_{i,D} \bar{h}_{i,D} \\ \dot{p}_G : q_{\dot{p}_{T^+,G}} = - \sum n_{i,G} \bar{h}_{i,G} \end{cases} \quad (18)$$

Notice that  $n_{i,*}$  are the stoichiometric quantities of the  $i$  compound in the  $*$  reaction, being positive for the reagents and negative for the products. The same process is applied to the entropy balance of each of the reactions, yielding the contributions presented in equation 19.

$$\begin{cases} \dot{p}_A : q_{\dot{\sigma},A} = -\frac{q_{\dot{p}_{T+,A}}}{T} - \sum n_{i,A} \bar{s}_{i,A} \\ \dot{p}_D : q_{\dot{\sigma},D} = -\frac{q_{\dot{p}_{T+,D}}}{T} - \sum n_{i,D} \bar{s}_{i,D} \\ \dot{p}_G : q_{\dot{\sigma},G} = -\frac{q_{\dot{p}_{T+,G}}}{T} - \sum n_{i,G} \bar{s}_{i,G} \end{cases} \quad (19)$$

These quantities, being obtained per presented reaction, can be converted into a more fitting base of amount of reserve consumed or produced, according to equation 20.

$$\begin{cases} \eta_{O_2,*} = \frac{n_{O_2,*}}{\mu_E n_{E,*}} \\ \xi_{T+,*} = \frac{q_{\dot{p}_{T+,*}}}{\mu_E n_{E,*}} \\ \gamma_* = \frac{q_{\dot{\sigma},*}}{\mu_E n_{E,*}} \end{cases}, \quad (20)$$

where \* is any one of assimilation, dissipation or growth reactions. The obtained values for all these couplers are presented in table 8.

Table 8: Dioxygen, dissipated heat, and entropy production couplers for the assimilation, dissipation, and growth processes.

	Assimilation	Dissipation	Growth	Units
$\eta_{O_2,*}$	$4.77 \times 10^{-7}$	$3.44 \times 10^{-6}$	$1.04 \times 10^{-7}$	mol.J <sup>-1</sup>
$\xi_{T+,*}$	-0.30	-2.03	-0.53	J.J <sup>-1</sup>
$\gamma_*$	$9.69 \times 10^{-4}$	$6.98 \times 10^{-3}$	$1.83 \times 10^{-3}$	J.J <sup>-1</sup> K

From here, the contributions of each of these processes can be equated for the full metabolism by multiplication with the respective power rate. For example, the dioxygen consumption flux can be fully quantified as

$$\dot{J}_{O_2} = \begin{bmatrix} \eta_{O_2,A} & \eta_{O_2,D} & \eta_{O_2,G} \end{bmatrix} \begin{bmatrix} \dot{p}_A \\ \dot{p}_D \\ \dot{p}_G \end{bmatrix} = \boldsymbol{\eta}_{O_2}^T \dot{\boldsymbol{p}}, \quad (21)$$

where  $\eta_{O_2,*}$  represents constant dioxygen consumption couplers that yield the amount of dioxygen associated to a given amount of energy,  $\dot{p}_*$ , spent on process \*.

The dissipated heat flux can be quantified as

$$\dot{p}_{T+} = \begin{bmatrix} \xi_{T+,A} & \xi_{T+,D} & \xi_{T+,G} \end{bmatrix} \begin{bmatrix} \dot{p}_A \\ \dot{p}_D \\ \dot{p}_G \end{bmatrix} = \boldsymbol{\xi}_{T+}^T \dot{\boldsymbol{p}}, \quad (22)$$

where  $\xi_{T+,*}$  represents constant heat dissipation couplers that yield the amount of heat dissipated for a given amount of energy,  $\dot{p}_*$ , spent on process \*.



Produced entropy  $\dot{\sigma}$  can then be quantified as

$$\dot{\sigma} = \begin{bmatrix} \gamma_A & \gamma_D & \gamma_G \end{bmatrix} \begin{bmatrix} \dot{p}_A \\ \dot{p}_D \\ \dot{p}_G \end{bmatrix} = \boldsymbol{\gamma}^T \dot{\boldsymbol{p}}, \quad (23)$$

where  $\gamma_*$  represents constant entropy production couplers that yield the amount of entropy production for a given amount of energy,  $\dot{p}_*$ , spent on process \*. Notice that  $\dot{J}_{O_2}$ ,  $\dot{p}_{T+}$ , and  $\dot{\sigma}$  are all explicit functions of constant values and  $\dot{\boldsymbol{p}}$ . These constant values depend only on the fixed stoichiometry of assimilation, dissipation and growth, and the fluxes' thermodynamic properties, while  $\dot{\boldsymbol{p}}$  is recursively obtained given feeding conditions and structural volume.



## 4 Applications

In this chapter, the presented model will be used to obtain results for individual biological systems<sup>1</sup> in terms of (i) dioxygen consumption, (ii) assorted metabolic power rates, (iii) both absolute and weight-specific production of irreversibilities, and (iv) reserve residence time. These variables were computed both for individual growth, in section 4.1, and the comparison of related species, in section 4.2. In this way, the basic assumptions of allometrically scaling entropy production and physiological time will be tested, as well as the consequent result of constant specific entropy production per physiological time lapse.

A sensitivity analysis for the presented results for certain parameters is also presented in section 4.3, namely for the somatic maintenance rate coefficient  $\dot{k}_M$ , the fraction of somatic maintenance and growth allocation  $\kappa$ , scaled length at birth  $l_b$  and at puberty  $l_p$ .

---

<sup>1</sup>The implementation of the model was done with the use of spreadsheets and the associated *Visual Basic for Applications* computational framework, responsible for the iterations made for increasing structural volume.

## 4.1 Intra-species results

The computation was made for four scaled reserve density levels, namely from  $e = 0.7$  to  $e = 1^2$ . The DEB model primarily models organism growth and development with length and consequently volume. However, in order to directly compare results with the literature, all figures are presented according to wet weight. The wet weight behaviour is presented in Figure 2.

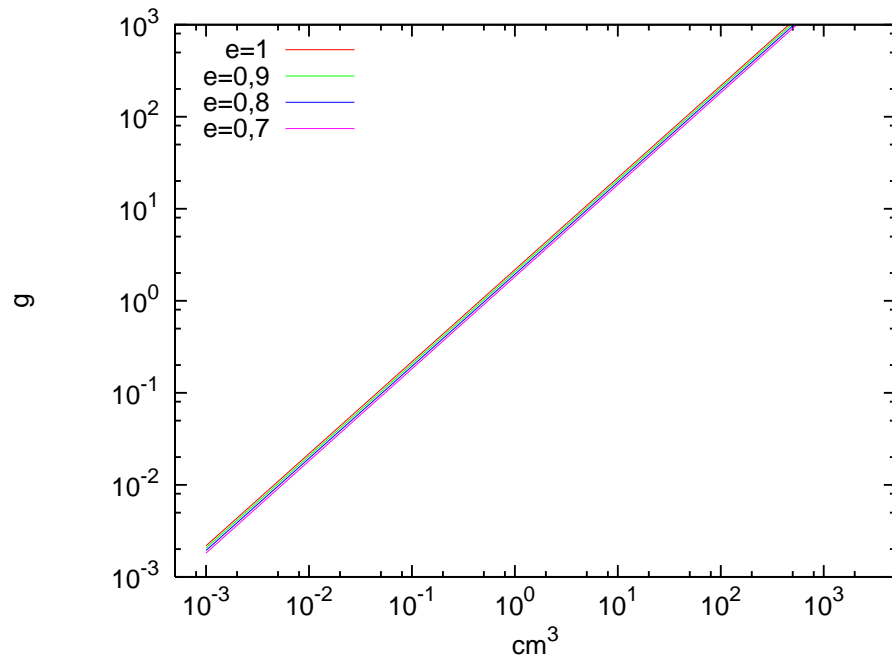


Figure 2: Wet weight vs. structural volume for varying reserve densities for the intra-species comparison

Wet weight is a straightforward variable in DEB, being influenced by increases in both structure and reserve, although reserve has a relatively small contribution. Notice that with higher access to food and the consequent higher energy reserve density, the organism is able to achieve larger volumes. Consequently, wet weight is not simply proportional to structural volume in a rigorous way, also depending slightly on the scaled reserve density. However, if scaled reserve density is constant throughout individual growth, wet weight can be seen as proportional to structural volume.

All other plots are for an individual with access to abundant food that yields  $e = 1$ . For example, the evolution of the three central power fluxes in the DEB organism,  $\dot{p}_A$ ,  $\dot{p}_D$ , and

---

<sup>2</sup>The structural volume values used were from an arbitrary initial volume of  $10^{-3} \text{ cm}^3$  to the organism's maximum volume in equally spaced points in a logarithmic scale, with mandatory calculations of the variables' values at birth and puberty.

$\dot{p}_G$ , are presented in Figure 3.

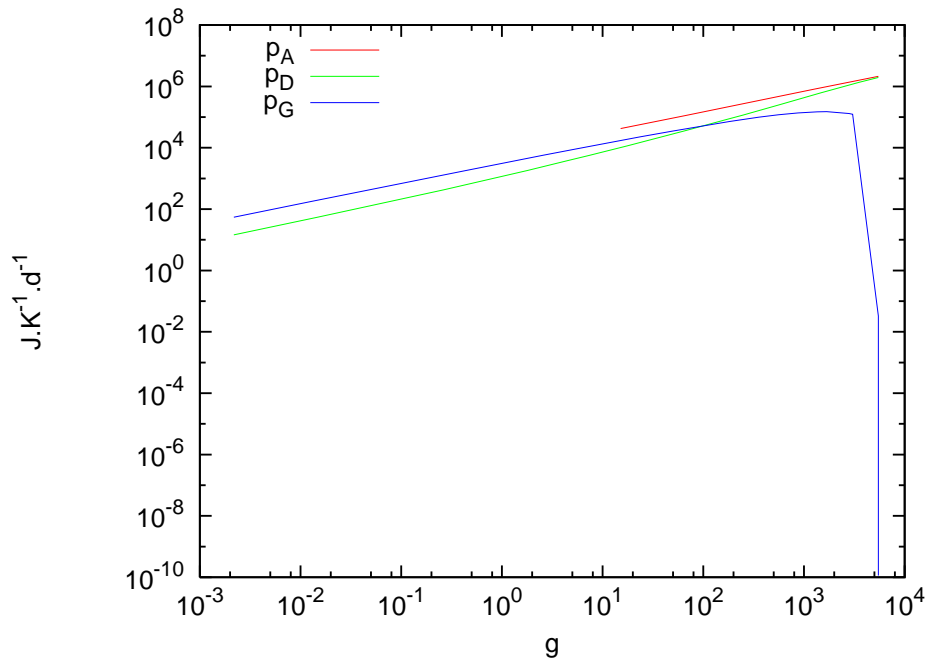


Figure 3: Assimilation, dissipation, and growth power rates vs. wet weight for the intra-species comparison

The major features of these behaviours is that growth increases until structural volume reaches its maximum and that the assimilation and dissipation power rates tend to equalize, as would be expected, in stationary state. Notice that, while assimilation and growth increase in a logarithmic parallel fashion, approximately following a  $2/3$  slope, at least until growth halts, the dissipation power rate increases with a higher slope that indeed increases throughout the organism, given the rise of importance of maintenance costs.

In Figure 4, the coherence of the usual representation of dioxygen consumption and the model results is visible.

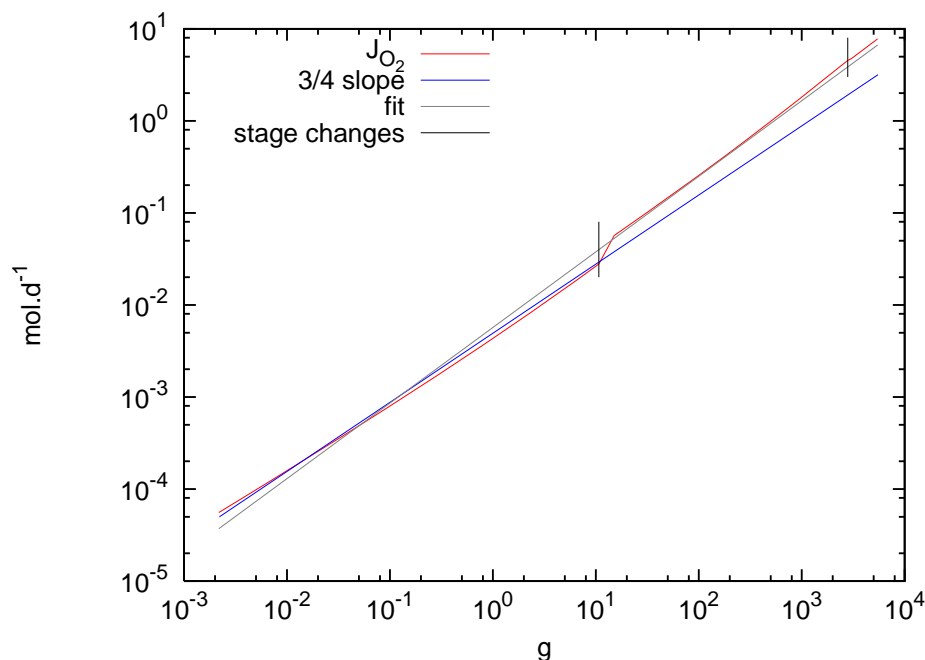


Figure 4: Dioxygen consumption rate vs. wet weight for the intra-species comparison

The bump of dioxygen consumption across birth is justified by the start of assimilation. Whereas usual allometry would predict a 0.75 slope, the statistical fit to the DEB model results is, in this case, described by a slope of approximately 0.82, majorly affected by the bump at birth. Such a high exponent value is consequent of the importance of the dissipation process, approximately proportional to structural volume, that shifts the weighted average toward a higher slope scaling behavior.

In Figures 5 and 6, the behaviour of  $\dot{p}_A$ ,  $\dot{p}_C$ ,  $\dot{p}_D$ , and  $\dot{p}_{T+}$  power rates are presented with the respective approximation potential fits. The mechanistically derived power rates evaluated do show some regularly sloped log-log lines, in particular assimilative and catabolic powers. However, these slopes are obtained as mechanistically fundamented variables, instead of statistically obtained regularities. Given their more general nature, they should be considered especially when evaluating species that do not fit the usual dioxygen consumption rate. Additionally, by representing variables affected by the species' parameter set, these power rates can theoretically explain in a consistent way the differences between dynamics of different metabolisms.

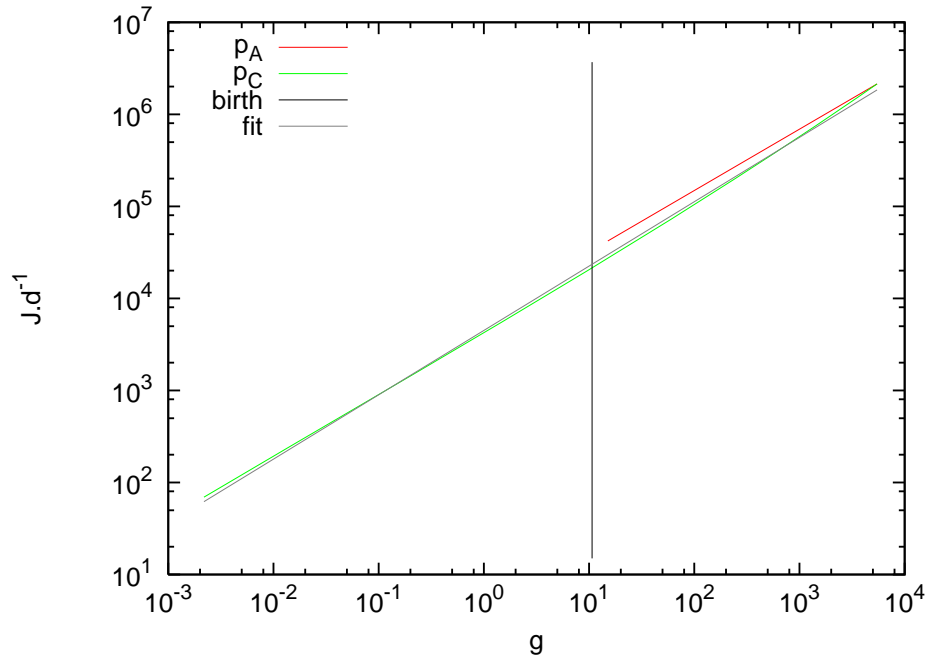


Figure 5: Power rates  $\dot{p}_A$  and  $\dot{p}_C$  vs. wet weight for the intra-species comparison

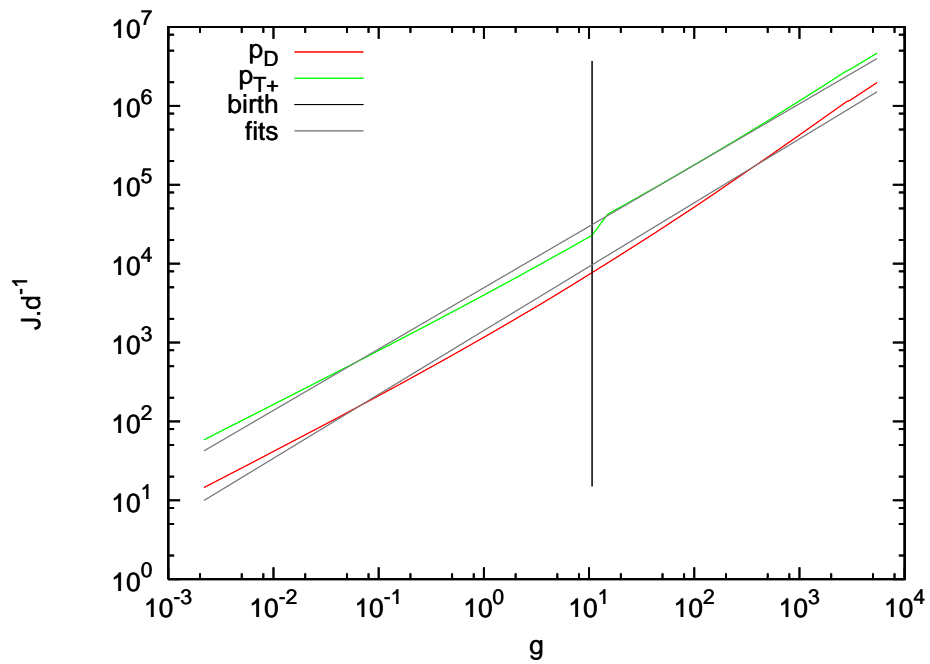


Figure 6: Power rates  $\dot{p}_D$  and  $\dot{p}_{T+}$  vs. wet weight for the intra-species comparison

These slopes, however, result from fundamental process differences: for example,  $\dot{p}_A$  presents a slope of  $2/3$ , given its direct proportionality with surface area by definition (see Table 7), while  $\dot{p}_C$  is resultant from different contributions either proportional to surface area or structural volume, originating a slope between  $2/3$  and  $1$  (Sousa et al., 2008). In this particular case, the best fit to  $\dot{p}_C$  is given by a power law with an exponent of  $0.70$ .

Notice that  $\dot{p}_{T+}$  is affected by birth given the start of the contribution from the assimilation process. Both the dissipative heat flux  $\dot{p}_{T+}$  and dissipation power rate  $\dot{p}_D$  have weaker but still reasonable fits to power laws, with  $0.78$  and  $0.80$  slopes, respectively. Such differences in slope are consequent of different processual foundations. While  $\dot{p}_{T+}$  results from the energy balance of the organism and therefore depends on the uptake and production of mineral and organic compounds,  $\dot{p}_D$  is a sum of the power allocated to maintenances (approximately proportional to structural volume) and to maturation or reproduction, that do not have any valid mechanistic description beyond being the last energetic priorities of the organism. Such mechanistic disconnection to any representative measure of size is the reason why their approximate logarithmic slopes are not intuitively explainable. Notice that the difference between these power rates yields the overhead costs of growth and assimilation.

In terms of entropy production, its absolute and mass-specific quantifications are present in Figures 7 and 8, respectively.

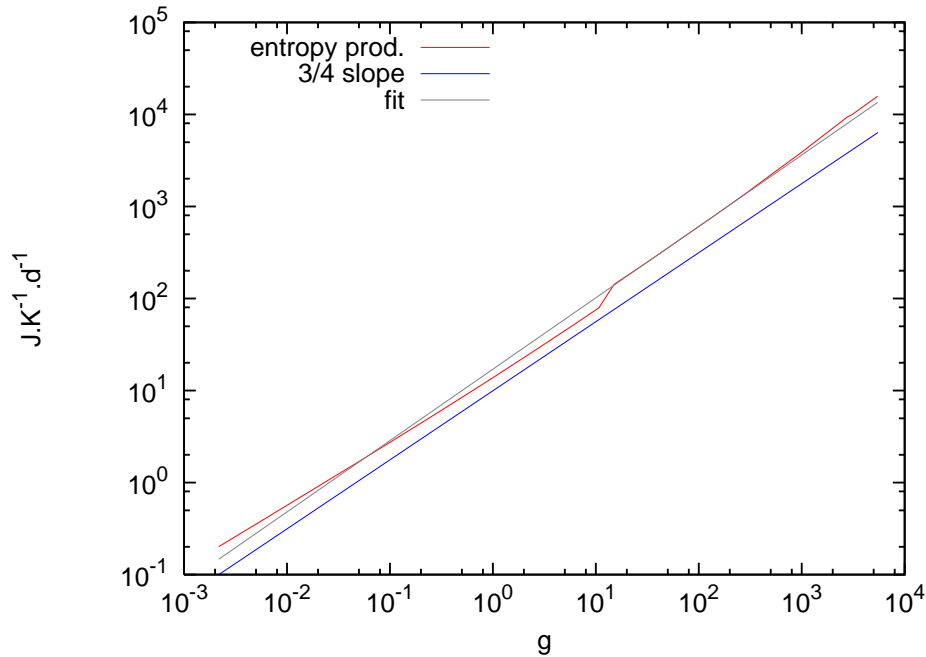


Figure 7: Absolute entropy production vs. wet weight for the intra-species comparison



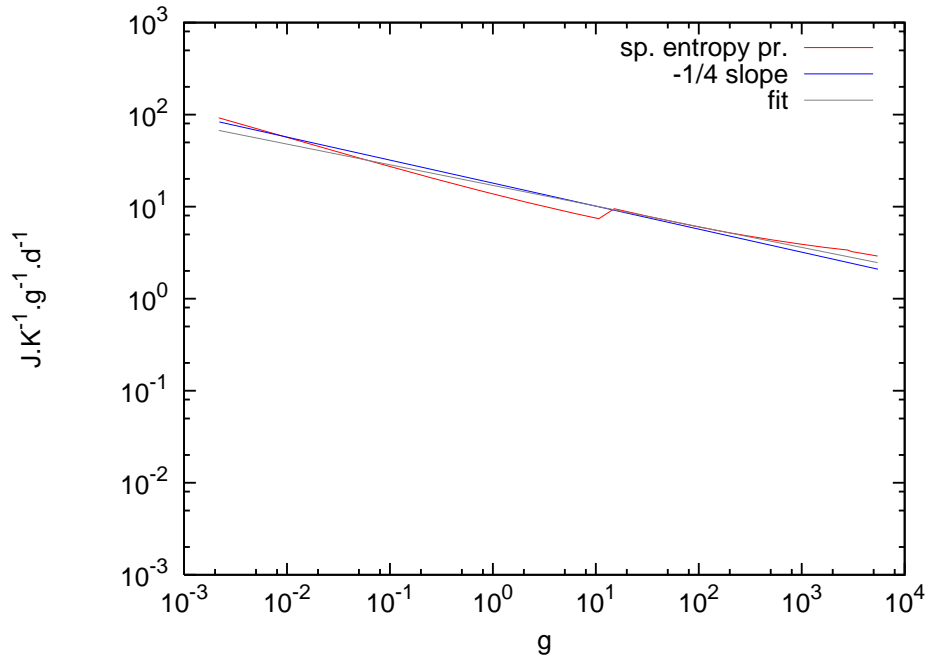


Figure 8: Specific entropy production vs. wet weight for the intra-species comparison

These results support the mentioned development behaviour in that the production of entropy increases and specific production lowers throughout the organism's life-cycle, in particular its late stages. These behaviours are generally fitted by the lines presented, defined by the slopes 0.78 and  $-0.22$ , respectively for absolute and weight specific entropy production. Also, another important results from referred figures is that absolute entropy production increases under proportionally to weight. Such result is a necessary consequence of the relation of entropy production with energy use and transformation; given that these processes scale proportionally to somewhere between  $W_w^{2/3}$  and  $W_w$ , so does the production of entropy.

Notice that the behaviours of  $\dot{\sigma}$  and  $\dot{p}_{T+}$  are similar. This similarity results from the low significance of the entropy trade-off, i.e., the difference between the mass inputs' and outputs' entropy values; such had already been found for aerobic metabolisms (Sousa et al., 2006). Hence, the irreversibilities generated by the macro-chemical reactions,  $T\Delta s$ , are negligible compared to the change in enthalpy,  $\Delta h$  Garby and Larsen (1995), which simplifies the entropy balance of the organism to  $T\dot{\sigma} \approx -\dot{p}_{T+}$ . Again, the behaviour is mainly affected by the initiation of assimilation, as presented in Figure 9.

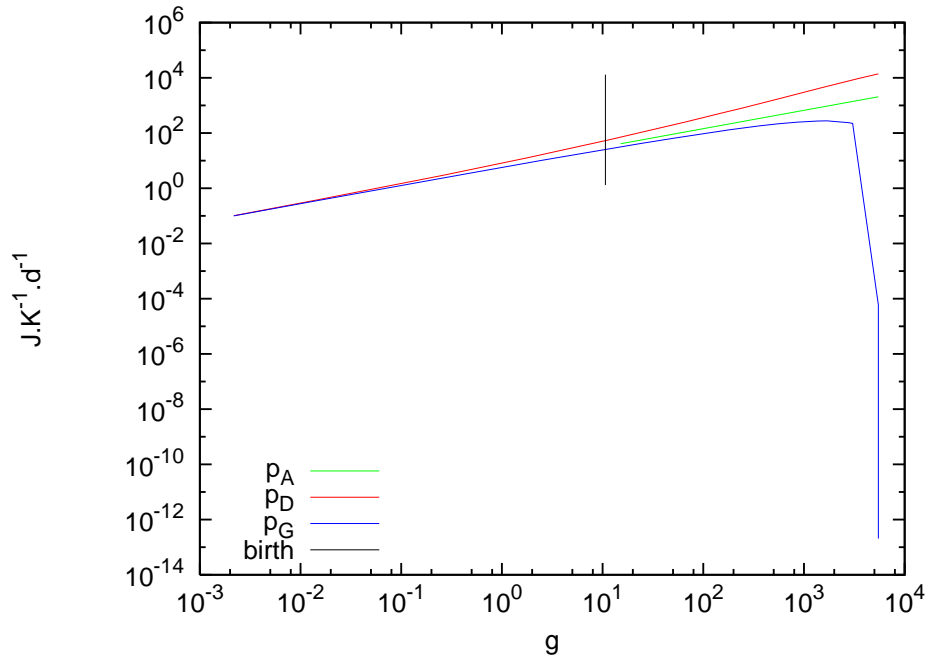


Figure 9: Contributions towards total entropy production vs. wet weight for the intra-species comparison

For metabolisms that have sharper contrasts on entropic contents being exchanged with their environment, as well as for metabolisms characterized by at least some endothermic reactions, this connection between dissipated heat flux and entropy production necessarily becomes more tenuous.

The physiological time lapse, reserve residence time  $t_E$ , follows the behaviour presented in Figure 10.

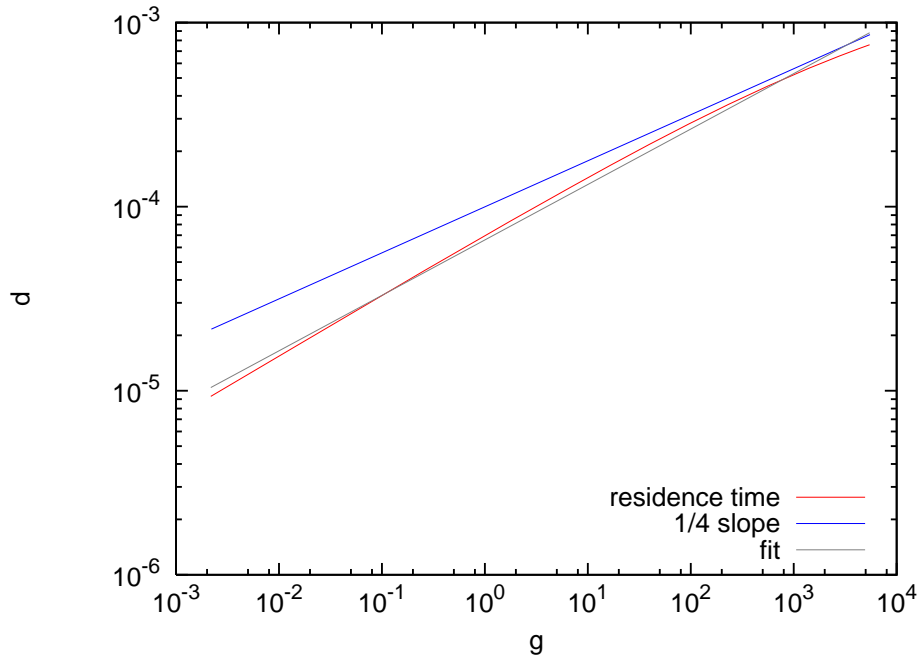


Figure 10: Reserve residence time vs. wet weight for the intra-species comparison

Reserve residence time shows a relatively small deviation from the  $W_w^{1/4}$  proportional power law, evolving closer to a 0.30 slope line in this particular model. This behaviour for the physiological time rate implies that, as expected, a given organism uses its energy in somewhat faster ways at the start of its life, decreasing reserve renewal rate for higher weights.

The deviations identified for  $t_E$  compound with those from  $\sigma$ , originating implications in the expected constancy of entropy production in the organism's physiological time scale, as can be seen in Figure 11. Additionally, the power laws for both variables have non-symmetric exponents, which leads to a non-constant multiplicatively aggregated power law.

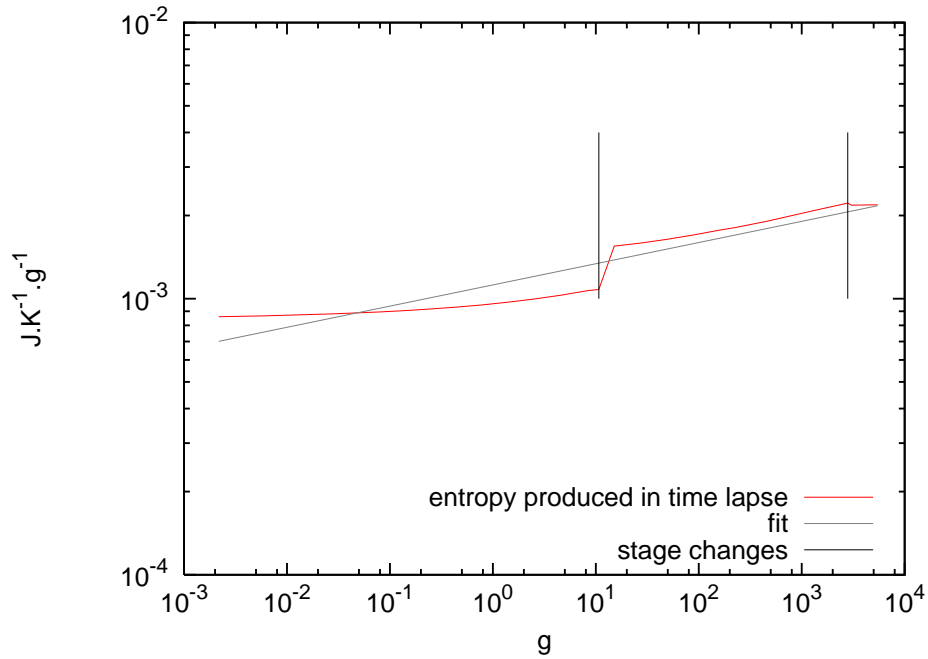


Figure 11: Specific entropy production in a reserve residence time lapse vs. wet weight for the intra-species comparison

Notice that “stage changes” corresponds to birth and puberty, in that natural order. Instead of being constant throughout individual growth, the amount of specific entropy produced in the reserve residence time scale,  $t_E \frac{\dot{\sigma}}{W_w}$ , declines with body mass with a poorly representative slope of 0.08. According to the presented curve, birth has an undeniable effect on the production of entropy per unit of wet weight.

This result is majorly determined by the initiation of assimilation at birth, introducing a discontinuity in the production of entropy that would otherwise not be considered. Additionally, the slight variation of this value is promoted by changes in contributions from assimilation, dissipation and growth, as can be seen in Figure 3. Again, this results underlines the dominance of the dissipation process towards the production of entropy.

In order for  $t_E \frac{\dot{\sigma}}{W_w}$  to be constant, the external mass fluxes have to be balanced, which only happens approximately in the embryo life phase of the modelled organism.

## 4.2 Inter-species results

Variable values were calculated iteratively for the general conditions of an inter-species analysis<sup>3</sup>. Notice that, instead of the previous plots, the evolution of volume or mass in these analyses does not represent growth in any way; instead, it represents slightly different, but related, species, that differ in maximum structural volume and consequently in maximum wet weight.

According to the presented model and reference parameter values, and for a fully grown ectothermic organism with access to abundant food, catabolic mobilisation power and assimilation power are identical. As such, the behaviour of all DEB power rates are presented in Figure 12.

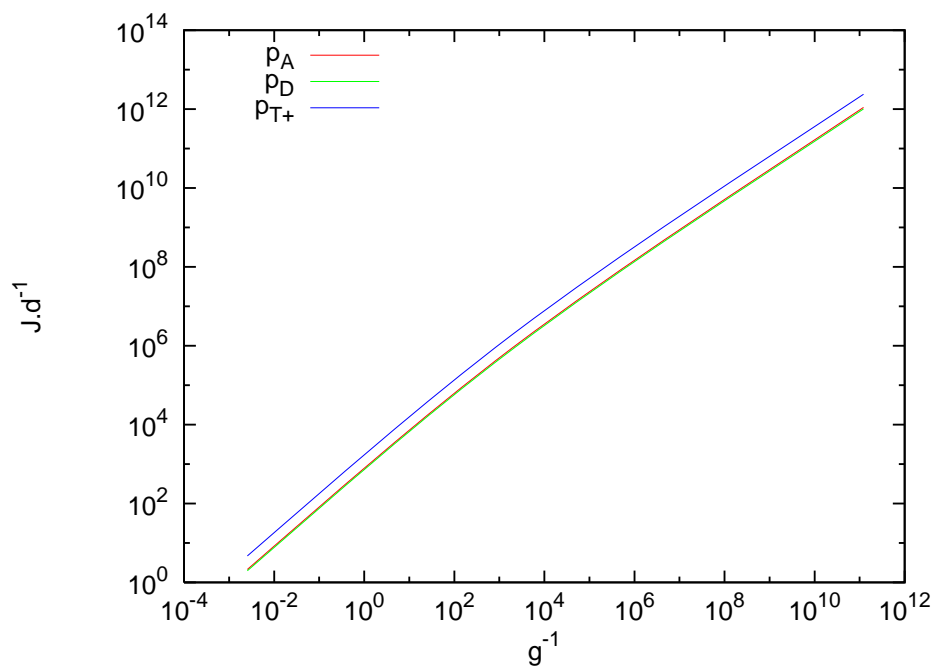


Figure 12: Power rates  $\dot{p}_A = \dot{p}_C$ ,  $\dot{p}_D$ , and  $\dot{p}_{T+}$  vs. wet weight for the inter-species comparison

The equivalence of  $\dot{p}_A$  and  $\dot{p}_D$  is justified by the consideration of steady state for the organisms i.e., all assimilated energy is dissipated, given the condition of full growth.

All the presented power rates follow the same general behaviour concordant with the 3/4 power rule; the measured exponent value is closer to 0.85, although the behaviour is not linear in logarithmic scales. Notice that, although the dissipative heat flux  $\dot{p}_{T+}$  deviates

<sup>3</sup>The maximum structural volume values used were from  $V_m = 2.5 \times 10^{-3} \text{ cm}^{-3}$  to  $V_m = 1.3 \times 10^9 \text{ cm}^{-3}$ , in equally spaced points in a logarithmic scale

from the remaining energy fluxes in this inter-species analysis, a close correlation exists in the way these variables behave with growth, indicating that all of them are affected in the same way by changes in maximum structural volume.

Again, these behaviours' approximated slopes arise from a compromise between surface and volume related processes, but in this case these values are resultant from a weighted sum of the contributions of either constant primary or design primary parameters to the variables' behaviour. The equal slopes for all the variables in Figure 12 indicates that all of them are affected in similar weights by these two sets of parameters.

However, these variables all exhibit a strong deviation from what would otherwise be a very smoothly sloped line. This deviation is motivated by the variation of the amount of reserve in proportion to structural volume. A single organism does not change this proportion as long as the scaled reserve density remains constant through growth. On the contrary, even for the conditions defined earlier of full access to food, the inter-species analysis introduces variability in the ratio between reserve and structure because the maximum reserve density is a physical design parameter and as so increases with  $V_m$ . This creates a situation in which reserves represent an increasing slice of the metabolism, distorting the behaviour of the analysed metabolic variables. As maximum volume increases, the represented species have higher reserves, stabilizing the evolution of the variable at a relatively constant sloped line, that is astoundingly close to the expected allometric slope.

The absolute entropy production variation with wet weight is presented in Figure 13, while Figure 14 presents the evolution of the specific entropy production.

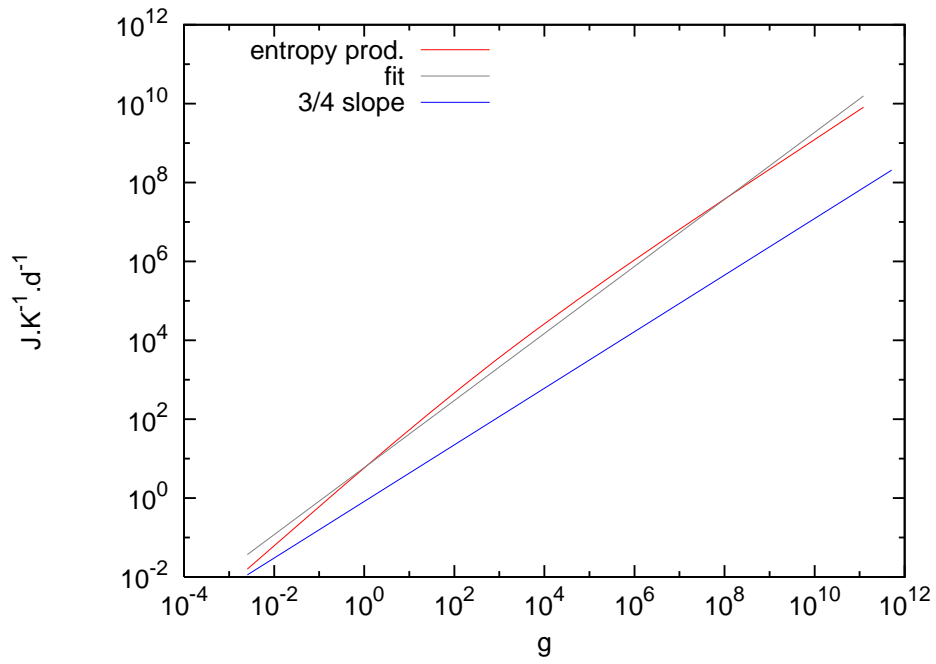


Figure 13: Absolute entropy production vs. maximum wet weight for the inter-species comparison

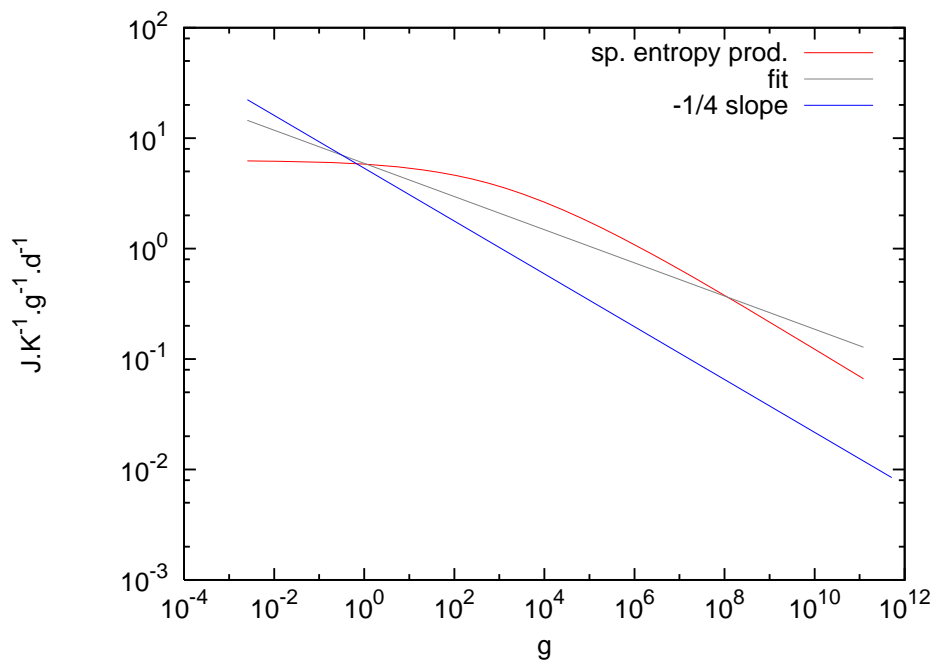


Figure 14: Specific entropy production vs. maximum wet weight for the inter-species comparison

Absolute entropy production describes a behaviour similar to those described by the as-sorted power rates, connecting their mechanical backgrounds. In fact, the slope of the allometrical fit is the same, 0.85, indicating that all these processes are again affected in the same way by changes in maximum volume. This results supports in part the assumption made by Andresen et al. (2002) of equivalence between metabolic rate and entropy production.

However, specific entropy production shows some deviation from the expected slope, particularly for smaller species, in such a way that its behaviour is not satisfactorily described by a power law approximation, that in this case yields a slope of  $-0.15$ . Both of these behaviours are, concordantly with all the other variables, affected by the small scale species' effect of decreased presence of reserves.

Figure 15 presents the contributions towards total entropy production from assimilation and dissipation, once in inter-species analysis there is no investment in growth.

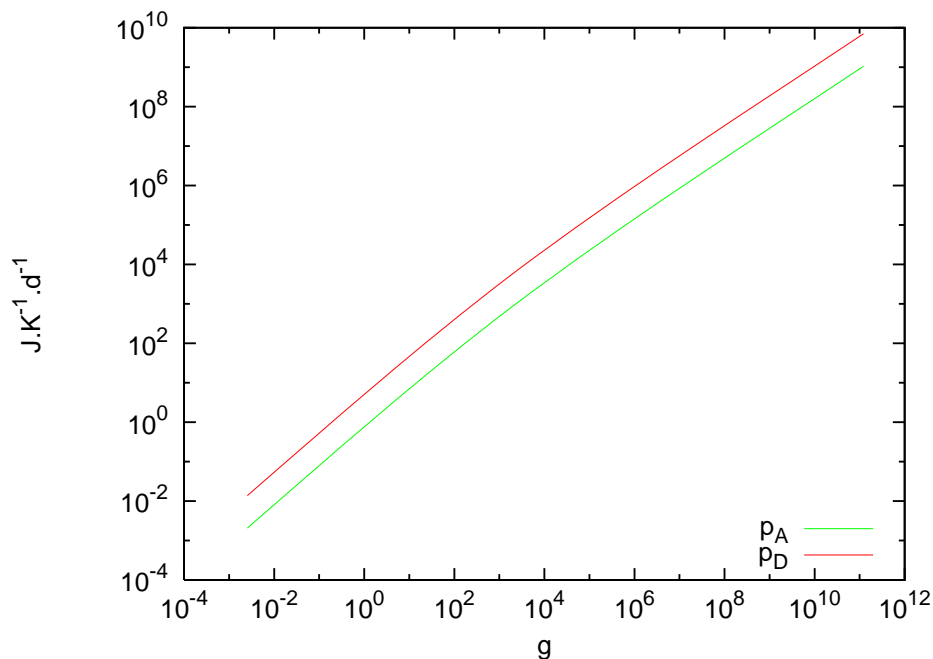


Figure 15: Contributions towards total entropy production vs. wet weight for the intra-species comparison

These contributions maintain proportionality between one another for species of all sizes, which illustrates the relevance of the constant cellular parameters towards entropy production in the modeled organism.

The evolution of reserve residence time lapse across related species is presented in Figure 16.



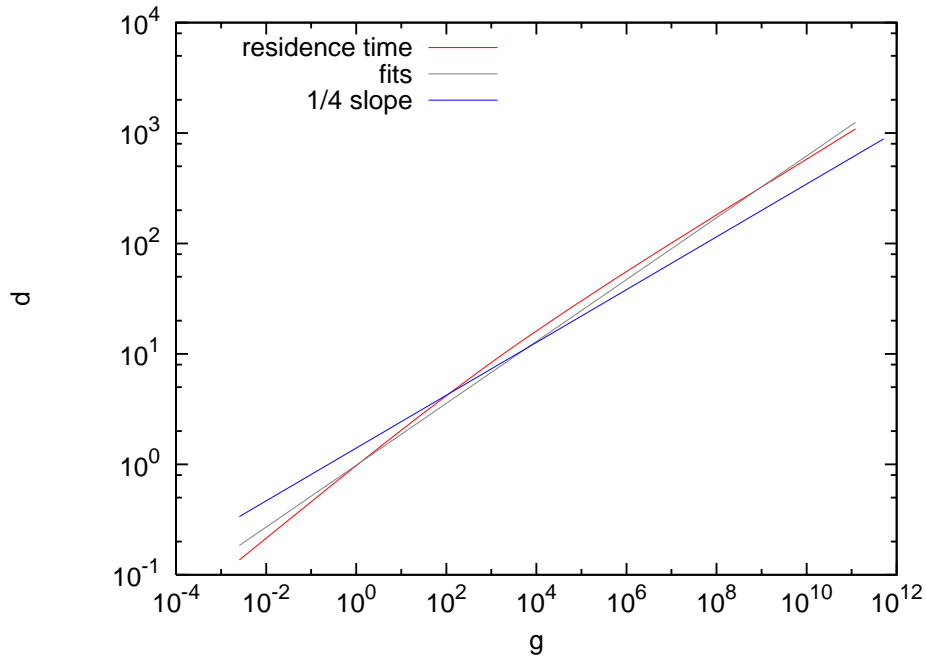


Figure 16: Reserve residence time vs. maximum wet weight for the inter-species comparison

Reserve residence times follow approximately the behaviour predicted by the  $-1/4$  power scaling law, with its statistical fit yielding a slope of 0.28, with a fit better than that obtained for the intra-species analysis. Again for physiological time, inter-species analysis turns out to be better approximated by power laws than intra-species. However, notice that the respective slope value is not obtained from the reciprocal of any power rate, contrarily to what happens in the intra-species analysis.

The evolution of specific production of entropy  $\dot{\sigma}/W_w$  in the reserve residence time lapse is presented in Figure 17.

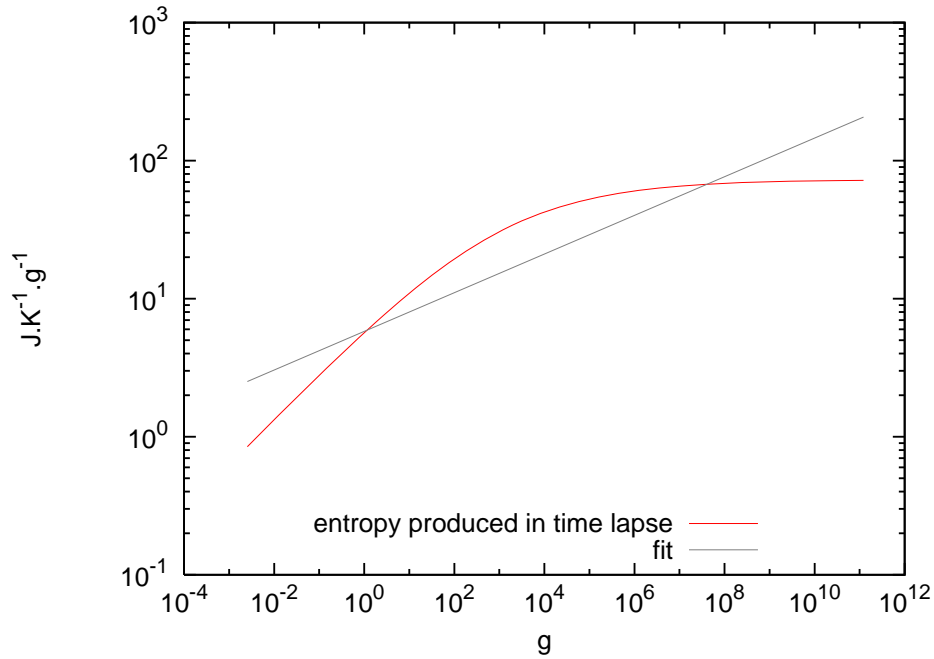


Figure 17: Specific entropy production in a reserve residence time lapse vs. maximum wet weight for the inter-species comparison

As would be obtainable from previous results, the slope of the approximation to this variable is  $-0.15 + 0.28 = 0.14$ , which is slightly different from the expected, although for large body weights this variable tends to a constant value. Again, this deviation results from the deviations registered for  $\dot{\sigma}/W_w$  in Figure 14 and  $t_E$  in Figure 16.

The deviation that this variable shows from an expected constant value is focused on the lower end of the tested weight spectrum, where reserve has a relatively less important part of the total weight as has already been seen for other variables. For those smaller species, scale does not influence the specific production of entropy in the physiological time scale, contradicting results by Andresen et al. (2002).

### 4.3 Sensitivity analysis

The presented results were obtained for the parameter values presented in page 27. In order to assess their sensitivity to parameter changes, a set of key parameters were changed, namely the somatic maintenance rate coefficient  $\dot{k}_M$ , the allocation fraction to somatic maintenance and growth  $\kappa$ , and scaled lengths at birth and puberty  $l_b$  and  $l_p$ .

These parameters were chosen because of their importance for the internal processing of energy, in particular the allocation and development strategies of the organism. On one hand, the effects of different maintenance costs were tested by varying  $\dot{k}_M$ , while different allocation strategies were modelled with varying  $\kappa$  values. The tests for different maturity threshold values were made in order to assess the level of affectability of the obtained results to different development patterns.

The considered values for the sensitivity analysis are presented in Table 9, being tested independently.

Table 9: Extreme values used for the sensitivity analysis

Value	$\dot{k}_M$	$\kappa$	$l_b, l_p$
Low	0.01 d <sup>-1</sup>	0.20	0.05, 0.20
Medium	0.05 d <sup>-1</sup>	0.80	0.125, 0.80
High	0.20 d <sup>-1</sup>	0.99	0.60, 0.90

#### 4.3.1 Intra-species analysis

**Somatic maintenance rate coefficient** This parameter represents the ratio between somatic maintenance costs and new structure costs, mathematically defined in page 25. Consequently, higher values of  $\dot{k}_M$  imply a decrease in maximum volume, once the available energy for new growth decreases. This behaviour is presented in Figure 18 with the evolution of the catabolic mobilisation power according to wet weight.

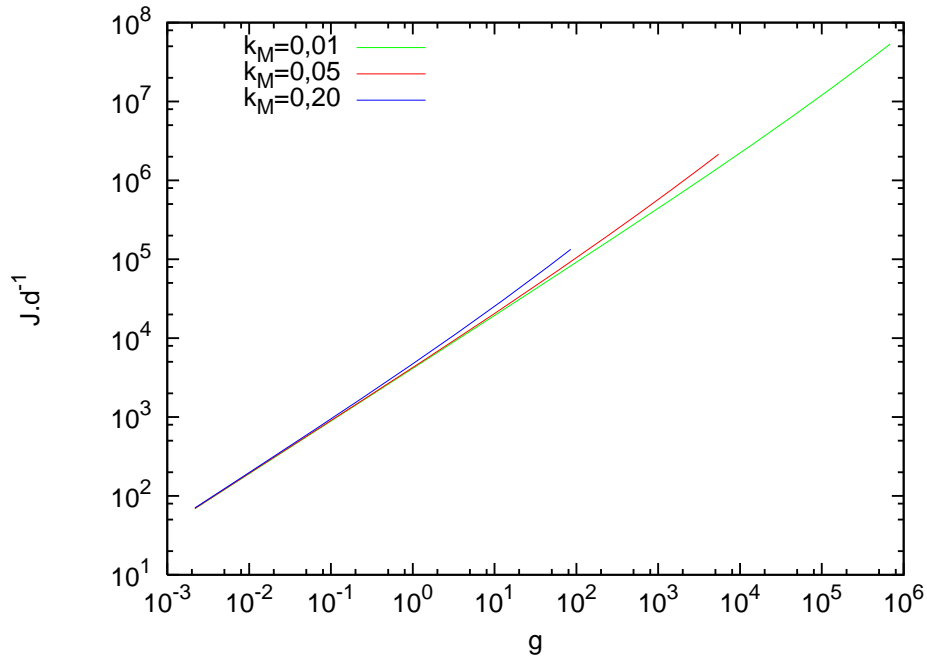


Figure 18: Catabolic power vs. wet weight for three different values of  $\dot{k}_M$

As presented, power rate for the intra-species comparison increase slightly in slope, according to the values presented in Table 10.

Table 10: Extreme values used for  $\dot{k}_M$  sensitivity analysis and resultant  $\dot{p}_C$  allometric approximation exponents

Value	$\dot{k}_M$	$\alpha$	$R^2$
Low	0.01 d <sup>-1</sup>	0.69	1.000
Medium	0.05 d <sup>-1</sup>	0.70	0.999
High	0.20 d <sup>-1</sup>	0.71	1.000

Given the close correlation of all three cases with the respective potential regression, the form of the curve is effectively maintained, only barely changing in logarithmic slope.

Nevertheless and aside from the changes of scales associated with different maximum volumes, all the obtained variables behave in much the same way as those presented earlier, including relative positions. Consequently,  $\dot{k}_M$  does not influence in any significant way the conclusions draw from the main results.

The change in the somatic maintenance rate coefficient changes the point of equilibrium between maintenance, growth and uptake in such a way that the organism is only viable at lower sizes. Although it would seem that the distribution of energy to the different activities would be subject to change for organisms differing only in  $\dot{k}_M$ , the truth is this only changes

the attainable maximum volume and consequently the energetic scale of the organism. This is consequent from the assumption that  $\dot{k}_M = \dot{k}_J$ , implying that both maintenances are proportional and that the ratio between all maintenance costs and all other investments is equivalent. Therefore, the distribution of energy in the organism is not affected by different values of  $\dot{k}_M$ .

An interesting result arises from the comparison of the obtained curves for weight specific entropy production,  $\dot{\sigma}$ , for the presented values for  $\dot{k}_M$ , presented in Figure 19.

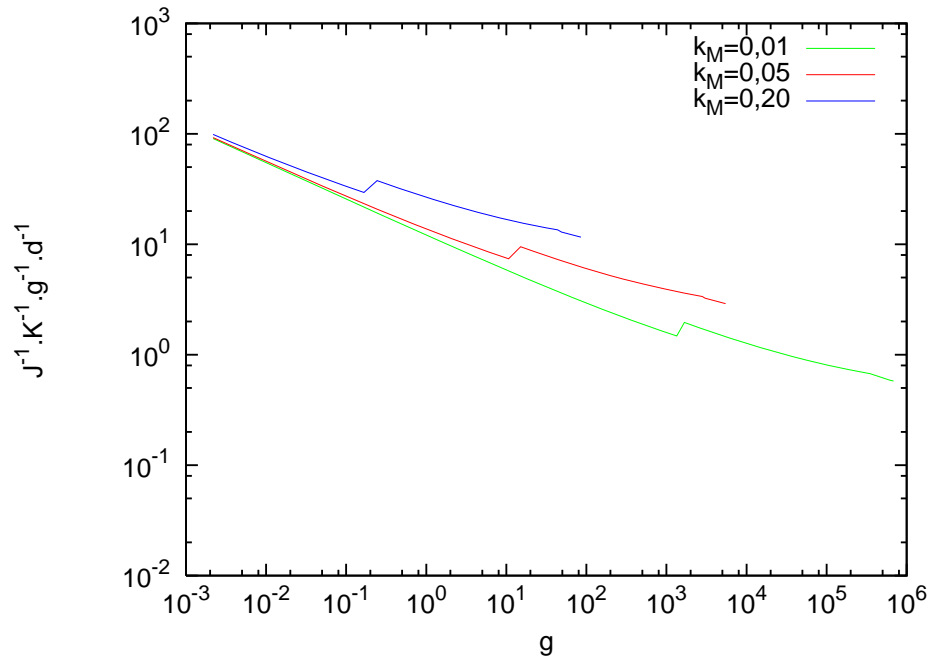


Figure 19: Specific entropy production vs. wet weight for three different values of  $\dot{k}_M$

Notice that the curves are similar to one another, although spanning different sizes. Additionally, for higher values of  $\dot{k}_M$  specific entropy production increases.

As seen, such behaviour cannot be due to any change in distribution of energy activities, once the allocation fraction remains the same. It can be concluded that, if the parameter allow it, this type of species compensates its large production of entropy with larger-sized bodies.

**Allocation fraction of catabolic power to somatic maintenance and growth** This parameter describes the fraction of catabolically mobilised energy that goes into somatic maintenance and growth, as described by the scheme on page 24. Catabolic mobilisation power reacts to changes in  $\kappa$  as presented in Figure 20, given the change in available energy for growth.

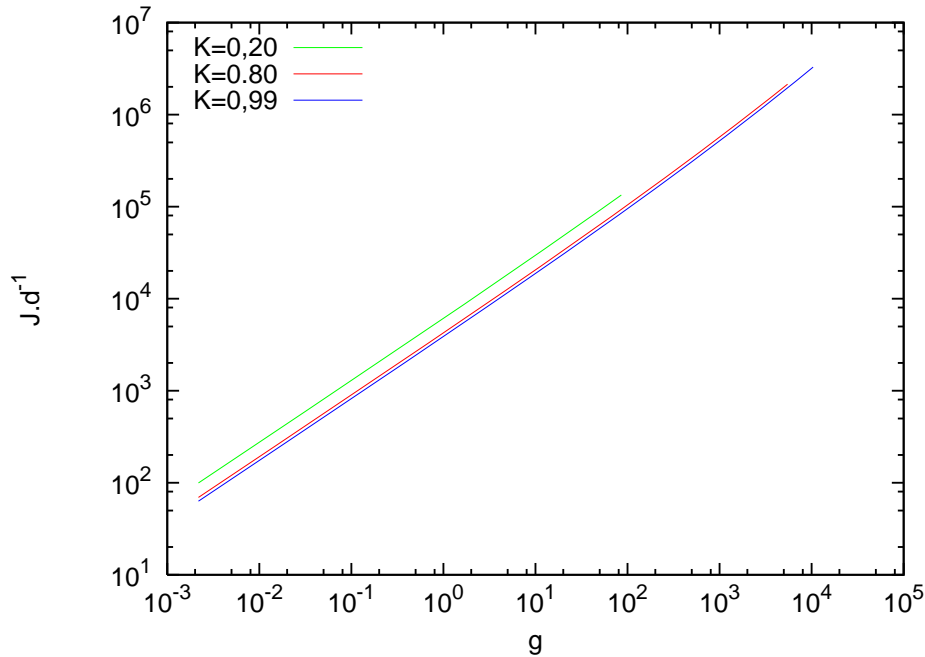


Figure 20: Catabolic power vs. wet weight for three different values of  $\kappa$

Although it is not apparent, increasing values of  $\kappa$  slightly increase the allometric power of the approximation to  $\dot{p}_C$ , as presented in Table 11.

Table 11: Extreme values used for  $\kappa$  sensitivity analysis and resultant  $\dot{p}_C$  allometric approximation exponents

Value	$\kappa$	Allometric $\alpha$	$R^2$
Low	0.20	0.68	1.000
Medium	0.80	0.70	0.999
High	0.99	0.70	0.999

Higher values of  $\kappa$  imply allocation strategies that prioritize somatic maintenance and growth in detriment of maturation and reproduction. For these cases, metabolic rates slightly increase their intra-species log-log slope, pointing to a higher importance of volume proportional costs, whereas the allocation to maturity and reproduction is lower, which activities have indeterminate proportionalities to structural volume. In another, more indirect way, if more energy is available for growth, the volume achieved is higher, resulting in more maintenance costs for the organism. Once these costs are proportional to volume, the slope of these curves will be increasingly higher.

The curves appear to descend towards higher values of  $\kappa$ , apparently compromising this interpretation. However this only happens because, for the same wet weight, an organism

with a higher  $\kappa$  value is at a lower stage of development i.e., is younger than another with a lower  $\kappa$  value. Changes in  $\kappa$  lead to a slight increase in the approximation's log-log slope. This does not change the relative positions of all the resultant curves, and so the conclusions are not affected by this parameter.

The variation of the curve of specific entropy production with variation of  $\kappa$  is presented in Figure 21.

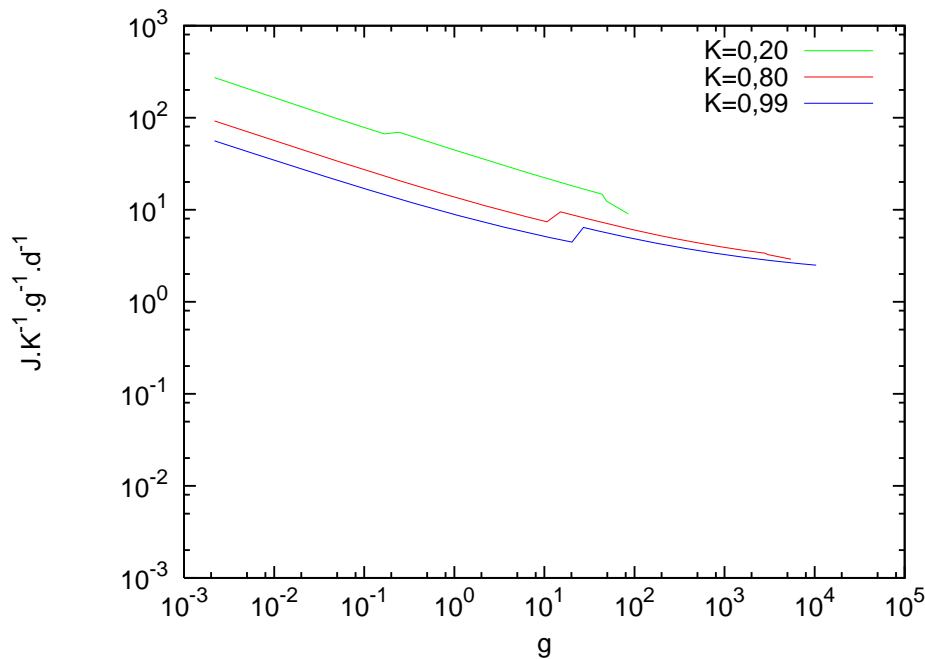


Figure 21: Specific entropy production vs. wet weight for three different values of  $\kappa$

In this case, the curves display similar behaviours stretched across different spans of wet weight, given that this parameter affects directly the organism's maximum structural volume. Again, the curves deviate from the previous slope at birth, by initiating feeding and defecation. Notice that curves for higher values of  $\kappa$  also register the same changes at puberty as the curve for the lower values. However, these changes are not so apparent because the energy being allocated to maturity or reproduction, the power rates affected by puberty, is comparatively small.

On the other hand, these curves are registered at different levels, which indicates that  $\kappa$  negatively affects the amount of entropy produced per wet weight of an organism i.e., higher values characterize organisms with lower specific productions of entropy.

With the knowledge that changes in the somatic maintenance rate coefficient do not affect the balance of activities taking place in the organism, while changes in the allocation constant do, we are now in good conditions to compare both sets of results in order to

identify which are conditions that produce more entropy. This comparison is presented in Figure 22.

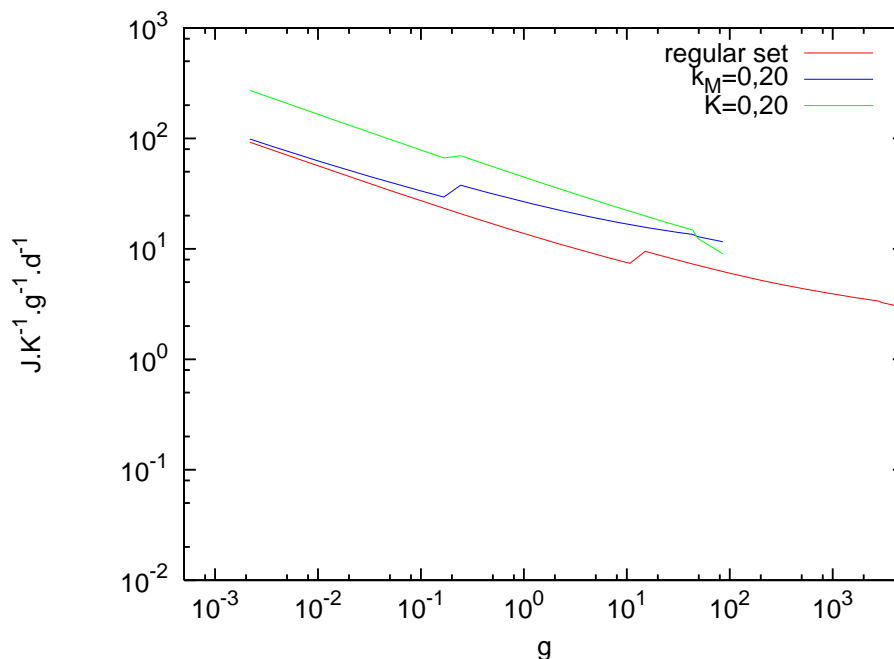


Figure 22: Specific entropy production vs. wet weight for three sets of parameters

Given a fortunate choice of parameter variations, the maximum structural volumes for the high  $\dot{k}_M$  value and for the low  $\kappa$  value are approximately equal to one another. From the presented figure, although the curves are not simple, some conclusions can be drawn.

For the low  $\kappa$  value, the different allocation strategy dictates higher specific entropy production. This is otherwise verified by the fact that, although both modified parameter sets lead to similar maximum structural volumes and correspondent entropy productions, the curve for the higher  $\dot{k}_M$  value has a higher entropy production during the growth phase. Given that the structural volume evolution is the same, phase transitions cease being a factor; in this case, only the allocation scheme can justify the identified differences in behaviour. Therefore, maturity allocation, both in investment and maintenance, is a relevant contributor to the production of entropy in the modelled organism, has had already been concluded from Figure 9 in page 46.

**Scaled length at birth and at puberty** Changes in life stage transitions are very important in biology. Although not explicitly,  $l_b$  and  $l_p$  reflect the species' development type.

Notwithstanding, the changes in scaled length at birth and puberty presented in Table 12



do not lead to relevant changes in results, with the only remarkable change being the translation of the bump in dioxygen consumption attributable to the start of assimilation.

Table 12: Extreme values used for  $l_b$  and  $l_p$  sensitivity analysis and resultant  $\dot{p}_C$  allometric approximation exponents

Value	$l_b$	$l_p$	$\alpha$	$R^2$
Low	0.05	0.20	0.70	0.999
Medium	0.125	0.80	0.70	0.999
High	0.60	0.90	0.70	0.999

Such translation is perfectly visible in Figure 23.

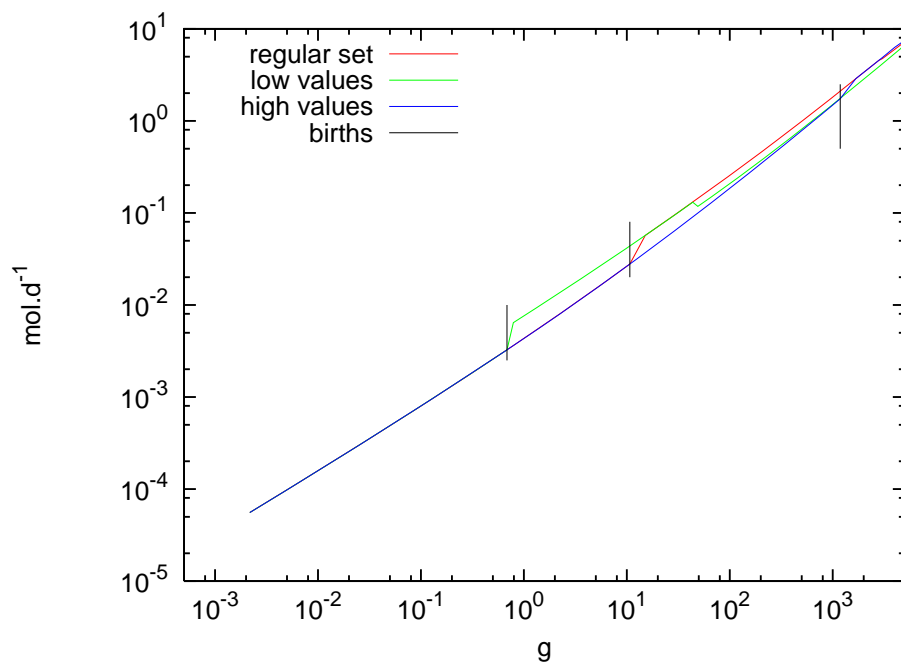


Figure 23: Dioxygen consumption flux vs. wet weight for the three sets of values of  $l_b$  and  $l_p$

### 4.3.2 Inter-species analysis

In terms of inter-species analysis, varying threshold scaled lengths are of no consequence given the focus on fully grown individuals. Consequently, the tested parameters were only  $\dot{k}_M$  and  $\kappa$ .

**Somatic maintenance rate coefficient** For the inter-species comparison, the obtained results hold whatever the value of  $\dot{k}_M$  is, including the exponent of allometric fit to  $\dot{p}_C$ , that is constant at 0.81. This means that the curves displayed in Figure 24 are approximated by parallel curves.

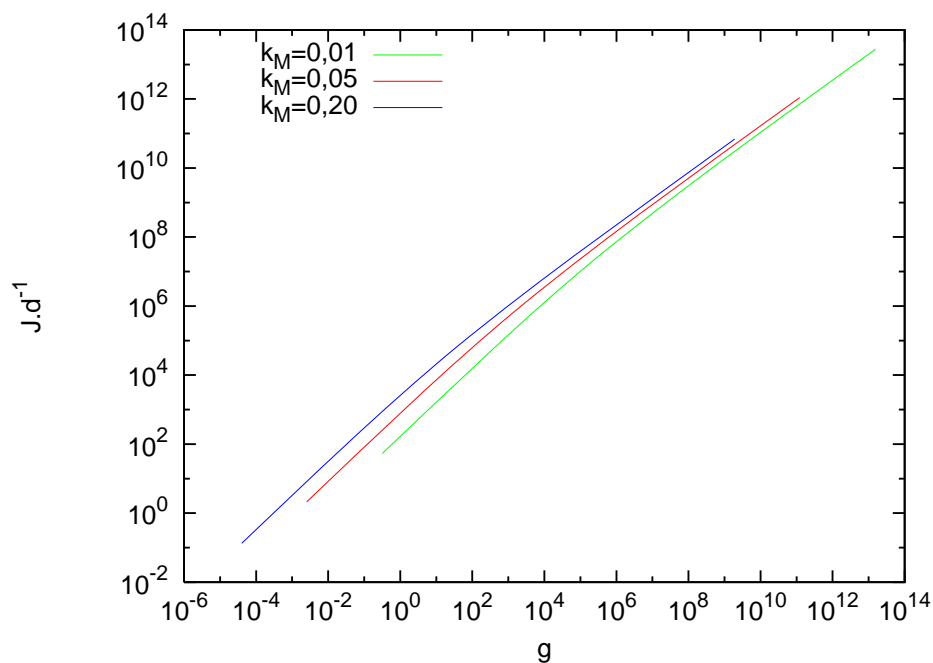


Figure 24: Catabolic power vs. wet weight for three different values of  $\dot{k}_M$  for the inter-species comparison

This result demonstrates the difference between comparing individual life cycles and comparing related species at maximum structural volume. While in the first case certain parameters, such as  $\dot{k}_M$ , influence the evolution of metabolic powers by changing the mix of contributing processes, in the particular case of inter-species analysis there is no consequence for the variation in these parameters. Of course, this is connected to the fact that, at this level of analysis, only fully grown organisms are compared, and so the analysis shows no effects whatsoever over growth and maintenances. For example, while the intra-species analysis follows the organism across a period that sees changes in allocated

energy, from structure or complexity building activities to maintenances, in inter-species the organism is already fully grown, which means that energy is only allocated to maintenances and reproduction.

In fact, only the normalisation constant  $\dot{p}_{C_0}$  changes in these regressions, while the exponent stays the same. The way compared species relate to one another is then not influenced by changes in  $\dot{k}_M$ .

**Allocation fraction of catabolic power to somatic maintenance and growth** Coherently with  $\dot{k}_M$ , changes in  $\kappa$  do not influence the inter-species results whatever the values are, apart from an expected translation, similarly to presented Figure 25.

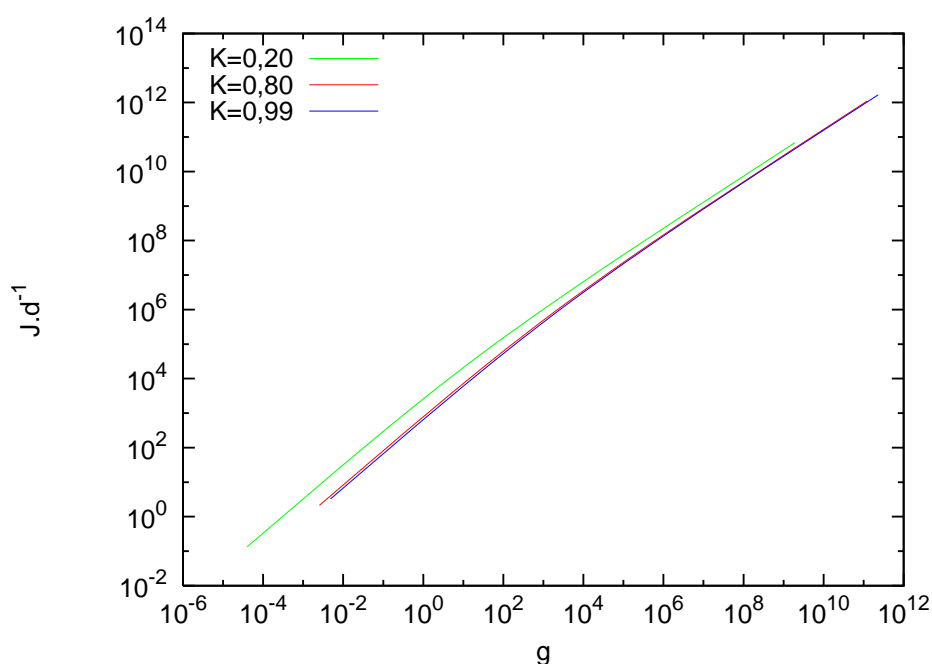


Figure 25: Catabolic power vs. wet weight for three different values of  $\kappa$  for the inter-species comparison

Such relative insensitivity is easily justified: both  $\kappa$  and  $\dot{k}_M$  are constant primary parameters, and as such are not affected by changes in the maximum structural volume; registered changes are only motivated by changes in the spatial and energetic scales of the modelled organisms.



## 5 Discussion

In this chapter, the results of the application of the presented DEB model will first be approached and discussed independently of the overarching discussion of energy and entropy in ecological and biological systems. Then, in page 68, the union of both studied aspects of these subjects will be made, in order to provide the closing arguments for the systemic equivalence between these systems.

**Results discussion** The obtained results point to a general adequacy of allometric approximations to dioxygen consumption and the main metabolic rates identified for the ectothermic aerobic species considered. These results are summarized in Table 13 where the variables are approximated by power laws given by  $V = V_0 W_w^\alpha$ .

Table 13: Parameter for obtained power law fits to variable evolution

Variable $V$	intra-species			Inter-species		
	$V_0$	$\alpha$	$R^2$	$V_0$	$\alpha$	$R^2$
$\dot{J}_{O_2}$	$6 \times 10^{-3}$	0.82	0.997	$3 \times 10^{-3}$	0.85	0.997
$\dot{p}_A$	$7 \times 10^3$	0.67	1.000	$8 \times 10^2$	0.85	0.997
$\dot{p}_C$	$4 \times 10^3$	0.70	0.999	$8 \times 10^2$	0.85	0.997
$\dot{p}_D$	$1 \times 10^3$	0.81	0.999	$7 \times 10^2$	0.85	0.997
$\dot{p}_{T+}$	$5 \times 10^3$	0.78	0.997	$2 \times 10^3$	0.85	0.997
$\dot{\sigma}$	17	0.78	0.997	5.9	0.85	0.997
$\dot{\sigma}/W_w$	17	-0.22	0.996	5.9	-0.15	0.910
$t_E$	$7 \times 10^{-5}$	0.30	0.997	1.0	0.28	0.997
$t_E \dot{\sigma}/W_w$	$1 \times 10^{-3}$	0.08	0.897	5.8	0.14	0.832

The coefficients of determination for the approximation fits are appropriate for most of the presented variables. However, given the fact that these fits are power rules displayed across large spectra of values, some variables are not satisfactorily described by them, and therefore the algebraical value of  $R^2$  can be somewhat optimistic. Such is the case for  $\dot{p}_{T+}$  and consequently all entropy associated variables. This is a larger problem for the intra-species analysis, given that, for the inter-species analysis, most variables behave similarly.

Such equivalence in the inter-species variable behaviour is justified by similar affectability to changes in design primary parameters, that depend on the physical scale of the organism. By being affected in similar ways by these parameters, the behaviours of some of the analysed variables, such as all the power rates and absolute entropy production, are equivalent.

Notice that these results identify a generally ignored incoherence of allometrical power laws: there is no distinction between individual growth and the comparison of different

species. The analysis of metabolisms and their intricacies would consequently benefit if correct amount of attention would be given to the right sets of parameters and data.

Another strong feature of the DEB model is the disaggregation of metabolic rates. With its level of disaggregation, the model can be relevant for different levels of analyses, purposes, and organisms. For example, while along the growth of a single organism all the analysed rates behave differently although in similar ranges, they all change equivalently with maximum wet weight between full grown related species. These important differences are not usually taken into account in allometry, in particular given the use of a single aggregated metabolic rate.

Some issues were uncovered regarding the production of entropy, in particular the assumption that it would be proportional to the metabolic rate represented by the dioxygen flux. The operative word in the last sentence is “the”, because it implies that the proportionality would apply to the only usually defined metabolic rate. As seen, all the identified metabolic rates behave differently, particularly so along an individual life cycle. In terms of entropy, the relevant power rate in aerobic organisms is indubitably  $\dot{p}_{T+}$ , given its similar theoretical genesis with  $\dot{\sigma}$  and the results referred in page 45. Hence, the assumption stating that entropy production scales like a general power rate for an individual is flawed because there is no such thing; different power rates scale differently throughout an individual organism’s life cycle and have different mechanistic meanings.

As would be expected in the inter-species comparison, entropy production is relatively well described by the allometrical approximations, given that  $\dot{p}_{T+}$  itself evolves similarly to all the other power rates. Consequently, energy transforming processes evolve similarly to dissipating processes throughout related species, which again implies that they are similarly affected by changes in design primary parameters.

In terms of the physiological time lapse, reserve residence time behaves in a way reasonably close to the allometric curve in both analyses. However, specific entropy production in the physiological time scale is not satisfactorily described by the allometric result i.e., this variable is not constant neither for individual growth nor for related species. However, these deviations are justified by different effects in intra and inter-species analysis.

In intra-species, such deviation is mostly connected to the start of assimilation, that introduces a new positive contribution to entropy production, as well as to the increase in the dissipation power rate.

For the inter-species comparison, these deviations are associated with the role of the reserves: the behaviour of specific entropy production in the physiological time scale tends to a constant value for large organisms because the maximum reserve density for these cases is higher than for lower weights. Also, given the fact that physiological time does not scale reciprocally to any power rate, the product of these two behaviours is consequently not constant.

These results do not contradict similar more general conclusions achieved within a more formal and fundamental thermodynamic result (Andresen and Gordon, 1994), because those results are valid for uniform systems (i.e. with no spatial gradients) with rigorously defined intensive variables, not necessarily so for extremely heterogeneous, out of equilibrium systems involving such complex dynamics as an organism.

Such result implies that it is the overly aggregative usual view of metabolism that produced the fallacious result in the first place: yes, the production of entropy behaves proportionally to a power rate, and yes, physiological time is related with a power rate, but they do so with different power rates, that quantify different mechanisms. Notice that this result only applies to organisms that do not maintain significantly skewed entropy trades with the surrounding environment, consequently exporting approximately all their entropic production via dissipated heat. With a higher skew of the mass fluxes' entropy values, it is expected that the internal production of entropy would need to be further limited in order to maintain the overall equilibrium.

The sensitivity analysis demonstrates the robustness of the results, although some minor changes in slope and position of the curves can be expected in certain conditions.

For the same final maximum structural volume, decreases in the allocation fraction constant lead to comparatively higher production of entropy than the equivalent change is the maintenance rate coefficient. This underlines the fact that maturity maintenance and investment and consequently the dissipation macro-chemical process is responsible for the higher production of entropy. This result is verified because the maximum structural volume and correspondent production of entropy are approximately equal for both sets of parameters.

Changes in life stage transition parameters do not influence the results in any meaningful way. For what concerns the inter-species comparison, no changes in parameters lead to significant changes in results, besides the necessary changes in maximum structural volumes.

A final word of note for the differences between the results of both levels of analysis. Both intra and inter-species comparisons yielded results explainable by a compromise between volume and surface specific factors. However, the crucial difference is that while an individual organism maintains its parameter values, changing variable values in consequence of the evolution of reserve and volume dynamics, maximally grown related species differ in certain parameter values, consequently resulting in different dynamics. This means that, while variable behaviour in intra-species is defined by compromises between contributing factors, in inter-species this behaviour is defined by compromises between constant and design primary parameters.

The major result from the set of presented applications is that theoretical advances can suffer from conceptual ambiguity of their basic assumptions. Definitions should be made carefully and clearly if knowledge is to emerge. The variety of processes involved in en-

entropy production in biological individuals complicate its full characterisation, being difficult to explain its development across individual growth and different species.

For the specific type of organism implemented, it was also found that the mass fluxes play an important role in entropy production and that, *ceteribus paribus*, higher allocation to growth leads to higher production of entropy.

Another important result is that exponents of allometrical fits for all the variables tested depend on the balance between surface and volume proportional processes, as had already been previously obtained (Sousa et al., 2008), either directly involving processes, in individual growth, or indirectly via the affecting parameters, for related species.

Consequently, in order to satisfactorily characterise metabolic scaling, all the contributing processes, in particular assimilation, dissipation, and growth, have to be quantified. In the particular case of the modeled organism, both aerobic and composed of exothermic chemical reactions, the usual metabolic quantifiers could be satisfactorily used. Although other types of organisms would definitely be more charismatic for the use of entropy production, in these cases the comparisons with usual measures would not be possible. This choice of organism was made to allow comparisons between the usual quantifiers of metabolic activity and entropy production.

**Connection to higher complexities** Within an holistic frame of reference, the presented results for organisms are coherent with the ecological goals for development. Hence, the concepts of ecosystem and organism are proven to belong to the same phenomenological class as dissipative structures. The fact that one is usually a component of the other does not take away any of the significance of this result; instead, it strengthens it. Besides being interconnected concepts, once ecosystems generally include organisms, these entities share a dissipative nature that determines their basic thermodynamics.

According to the model results, at one level of complexity, and some referred literature contributions, at the other, the mass and energy fluxes across the boundaries of these systems are determinant for their behaviours in terms of entropy production.

The model results also point to the importance of structural volume growth as a positive contributor to entropy production. Such result ties into the mentioned thermodynamic foundations of dissipative structures: these systems do increase absolute dissipative properties by increasing size, and do so with increasing importance for stronger investments in growth.



## 6 Concluding Remarks

In this work, the thermodynamic aspects of biologic life were followed for different levels of system complexity, namely the ecosystem and the organism.

At the ecosystem level, this work presents sets of guiding principles for the functioning, growth and development of ecosystems, in order to establish the state of the art in terms of the study of these systems from a general thermodynamic dissipative structure framework.

At a lower level, pertaining to individual organisms, a formal model for metabolisms, DEB theory, was used to obtain the evolution of some thermodynamic variables. These results were compared with usually used allometric scaling rules, tools that are rather acritically deemed appropriate for the description of metabolic aspects of organisms and the way they scale with body mass.

According to the presented model results, allometric approximations are satisfactory for some relevant variables, such as the dioxygen consumption rate, but have some problems with other subjects. Some of these problems derive from the level of concept aggregation in allometry, complicating its use for the achievement of sound, theoretically correct results. This is the case of a recent result that defends that specific entropy production in the physiological time scale is constant for all body masses and species (Andresen et al., 2002).

Catabolic mobilisation power, for example, follows a curve that can be satisfactorily approximated by an allometric power rule. The presented model has the advantage of incorporating a mechanistic basis, consequently allowing meaningful knowledge to be derived from its behaviour. These intricate variations can only be transmitted and explained by a theoretical model of the organism with disaggregated measures such as DEB theory.

For example, while allometric approximations are a good fit for the catabolic power rate, results drop quality for the dissipated heat flux. This is particularly relevant for the subsequent theoretical process that leads to the description of entropy production. As this variable is directly correlated to dissipated heat flux and not to catabolic power, its approximation as an allometric function of a metabolic rate similar to catabolic power is prone to generate confusion.

In terms of inter-species comparisons, all the power rates identified are approximated by a general allometric curve with the same exponent, although they do not describe linear behaviours in log-log plots. Consequently, in this case entropy production is satisfactorily described by allometry, albeit in an approximate way. The specific production of entropy in the physiological time scale is, however, not constant even across fully grown individuals of related species, given the deviations registered from the allometric approximations. These deviations are motivated by the increasing importance of reserve for the total weight of the organism, motivated by changes in associated parameters.

Any of these results are not relevantly affected by parameter variations, in particular  $\dot{k}_M$ ,  $\kappa$ ,  $l_b$  and  $l_p$ , although there are some changes registered with these variations. The slopes of catabolic power rates change with the allocation strategy, because the different energy using activities are proportional to different spatial elements. Also related to the allocation strategy, it was found that higher investments in growth lead to higher entropy production, but this can be more than compensated by an increase in size if maintenance is sufficiently low.

In conclusion, according to the presented theoretical model results, entropy was found to be just as good measure of metabolic activity as the more usual dioxygen consumption flux and dissipated heat flux, although all of them are described differently and behave differently with increasing mass. Notice that the usual measures are only valid for the modelled organism because it is both aerobic and based on exothermic macro-chemical processes only.

Generally, the described ecological goals for development were found to apply analogously for organisms. This is motivated by the equivalence between ecosystems and organisms from the dissipative structure point of view; although these concepts represent entities at different scopal ranges, they share thermodynamic imperatives. In conclusion, beyond being physically incorporated into one another, biological systems and ecological systems are analogously similar given the connection of their thermodynamic natures, defined by the urge to grow, develop and dissipate the maximum amount of energy.

**Future work** This work is, as any another, flawed and perpetually incomplete. Future work for this subject lies in three general directions: further particularisation of this specific implementation, expansion of applicability for other types of metabolisms and the crossing over of the concepts and approach into other systems.

The first field of advancement is relatively straightforward: the presented results can be improved with further particularization of parameter dynamics, full characterization of a suitable organism's features and activities, and further validation with equivalent studies in the literature. This work could also benefit from more analytical approaches in order to obtain clearer results. Additionally, extensive research could improve the results, for example by further specification of the simplifications made, such as assuming equal maintenance rate coefficients and ectothermicity, and by providing better estimations of compound compositions and properties.

Secondly, with the generalisation of the presented model into other types metabolisms and organisms, the achieved conclusions can be tested and generalised, or not, for wider ranges of examples. For instance, what would a similar work yield for an autotroph? In this sense, this work could be taken further with either more generalisations into larger realms of applicable examples.

The other field of advancement would take the approach displayed in this work and apply it into similar systems, either at other levels of biological life, such as populations or the biosphere, or at different types of systems altogether.

For example, there is an enormous field of intersection of the biological and ecological sciences with economics. With such common grounds, an equivalent of the presented formal model could certainly be devised for the growth development of economical structures. Similarly, the presented holistic principles of ecosystem growth and development can be transferred into economics. Realistically, the economy is just another level of stacked, interconnected systems inside the sphere of influence of a group of biological systems, and so the conversion of formal concepts from one set of dissipative structures to the other should be smooth. This development could play a large role in formalizing an approach for the recent field of industrial ecology. With either one of these developments, interesting insights could be provided for the mechanistic functioning of cities, companies, and economies, contributing positively for the formalisation of knowledge about the sustainability of human societies and structures.

In conclusion, the theoretical and mechanistical study of metabolism and energy in dynamic systems with dissipative properties is one of the most promising avenues for deepening human knowledge of any behaviour that presents these general traits, including our own.



## References

- Mohammad H. Akbari. Energy-based indicators of ecosystem health. Master's thesis, University of Guelph, Guelph, 1995.
- Timothy Allen and Thomas Hoekstra. *Toward a unified ecology*. Columbia University Press, 1992.
- Bjarne Andresen and J. M. Gordon. Constant thermodynamic speed of minimizing entropy production in thermodynamic processes and simulated annealing. *Proceedings of the National Academy of Sciences of the United States of America*, 99(9):5822–5824, 1994.
- Bjarne Andresen, J. S. Shiner, and Dominik E. Uehlinger. Allometric scaling and maximum efficiency in physiological eigen time. *Proceedings of the National Academy of Sciences of the United States of America*, 99(9):5822–5824, 2002.
- M. Austoni, G. Giordani, P. Viaroli, and Zaldivar J. M. Application of specific exergy to macrophytes as an integrated index of environmental quality for coastal lagoons. *Ecological Indicators*, 61(5):229–234, 2001.
- J. R. Banavar, J. Damuth, A. Maritan, and A. Rinaldo. Supply–demand balance and metabolic scaling. *Proceedings of the National Academy of Sciences of the United States of America*, 99:10506–10509, 2002.
- Simone Bastianoni, Federico Maria Pulselli, and Mauro Rustici. Exergy versus emergy flow in ecosystems: Is there an order in maximizations? *Ecological Indicators*, 6:58–62, 2006.
- E. Battley. An empirical method for estimating the entropy of formation and the absolute entropy of dried microbial biomass for use in studies on the thermodynamics of microbial growth. *Thermochimica Acta*, 326:7–15, 1999.
- Adrian Bejan. *Advanced engineering thermodynamics*. Cambridge University Press, 2000.
- Adrian Bejan. *Advanced engineering thermodynamics*. John Wiley and Sons, 2006.
- Charles M. Bishop. The maximum oxygen consumption and aerobic scope of birds and mammals: getting to the heart of the matter. *Proceeding of the Royal Society of London B*, 266:2275–2281, 1999.
- James Brown, James Gillooly, Andrew Allen, Van Savage, and Geoffrey West. Toward a metabolic theory of ecology. *Ecology*, 85(7):1771–1789, 2004.
- Mark Brown and Sergio Ulgiati. Energy quality, emergy, and transformity: H. t. odum's contributions to quantifying and understanding systems. *Ecological Modelling*, 178:201–213, 2004.

- William A. Calder. Ecological scaling: Mammals and birds. *Annual Review of Ecology and Systematics*, 14:213–230, 1983.
- Jafferson K. L. da Silva, Guilherme J. M. Garcia, and Lauro A. Barbosa. Allometric scaling laws of metabolism. *Physics of Life Reviews*, 3:229–261, 2006.
- Jafferson K. L. da Silva, Lauro A. Barbosa, and Paulo R. Silva. Unified theory of interspecific allometric scaling. *Journal of Physics A: Mathematical and Theoretical*, 40:F953–F959, 2007.
- Charles-A. Darveau, Raul K. Suarez, Russel D. Andrews, and Peter W. Hochachka. Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature*, 417:166–170, 2002.
- David W. Deamer. How leaky were primitive cells? *Nature*, 454:37–38, 2008.
- J. Dean. *Lange's Handbook of Chemistry*. McGraw-Hill, twelfth edition, 1979.
- P. S. Dodds, D. H. Rothman, and J. S. Weitz. Re-examination of the “3/4-law” of metabolism. *Journal of Theoretical Biology*, 209:9–27, 2001.
- Brian D. Fath, Bernard C. Patten, and Jae S. Choi. Complementarity of ecological goal functions. *Journal of Theoretical Biology*, 208:493–506, 2001.
- Brian D. Fath, Sven E. Jørgensen, Bernard C. Patten, and Milan Straskraba. Ecosystem growth and development. *BioSystems*, 77:213–228, 2004.
- Henry A. Feldman. On the allometric mass exponent, when it exists. *Journal of Theoretical Biology*, 172:187–197, 1995.
- Júlio Fonseca, Miguel Pardal, Ulisses Azeiteiro, and João Marques. Estimation of ecological exergy using weighing parameters determined from dna contents of organisms - a case study. *Hydrobiologia*, 475/476:79–90, 2002.
- L. Garby and P. Larsen. *Bioenergetics – Its thermodynamic foundations*. Cambridge University Press, 1995.
- Sven E. Jørgensen and Brian D. Fath. Application of thermodynamic principles in ecology. *Ecological Complexity*, 1:267–280, 2004.
- Sven E. Jørgensen, Søren Nors Nielsen, and Henning Mejer. Emergy, environ, exergy and ecological modelling. *Ecological Modelling*, 77:99–109, 1995.
- James J. Kay and Roydon A. Fraser. *Exergy analysis of ecosystems: Establishing a role for thermal remote sensing*. University of Waterloo, 2002.

- M. Kleiber. Body size and metabolism. *Hilgardia*, 6:315–353, 1932.
- B. W. Kooi and T. A. Troost. Advantages of storage in a fluctuating environment. *Theoretical Population Biology*, 70(4):527–541, 2006.
- S. A. L. M. Kooijman. *Dynamic energy and mass budgets in biological systems*. Cambridge University Press, second edition, 2000.
- S. A. L. M. Kooijman. Quantitative aspects of metabolic organization: a discussion of concepts. *Philosophical Transactions of the Royal Society B*, 356:331–349, 2001.
- S. A. L. M. Kooijman. *Dynamic energy and mass budgets for metabolic organization*. Unpublished, third edition, 2009.
- S. A. L. M. Kooijman. Personal communication, 2008.
- S. A. L. M. Kooijman, T. Sousa, L. Pecquerie, J. van der Meer, and T. Jager. From food-dependent statistics to metabolic parameters, a practical guide to the use dynamic energy budget theory. *Biological Reviews*, 83:533–552, 2008.
- J. Kozłowski and M. Konarzewski. Is west, brown and enquist’s model of allometric scaling mathematically correct and biologically relevant? *Functional Ecology*, 18:283–289, 2004.
- F. A. Labra, P. A. Marquet, and F. Bozinovic. Scaling metabolic rate fluctuations. *Proceedings of the National Academy of Sciences of the United States of America*, 104:10900–10903, 2007.
- R. C. Lasiewsk and W. A. Calder. Preliminary allometric analysis of respiratory variables in resting birds. *Respiration Physiology*, 11(2):152–166, 1971.
- Alfred J. Lotka. Contribution to the energetics of evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 8:147–151, 1922.
- J.E. Lovelock. A physical basis for life detection experiments. *Nature*, 207:568–570, 1965.
- J.C. Luvall and H.R. Holbo. *Thermal remote sensing methods in landscape ecology*. Springer-Verlag, 1991.
- A. M. Makarieva, V. G. Gorshkov, B.-L. Li, S. L. Chown, P. B. Reich, and V. M. Gavrillov. Mean mass-specific metabolic rates are strikingly similar across life’s major domains: Evidence for life’s metabolic optimum. *Proceedings of the National Academy of Sciences of the United States of America*, 105:16994–16999, 2008.
- Pablo A. Marquet, Fabio A. Labra, and Brian A. Maurer. Metabolic ecology: linking individuals to ecosystems. *Ecology*, 85(7):1794–1796, 2004.

- Philip Mirowski. *More heat than light, Economics as social physics, physics as nature's economics*. Cambridge University Press, 1989.
- R. M. Nisbet, E. B. Muller, K. Lika, and S. A. L. M. Kooijman. From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology*, 69:913–926, 2000.
- H.T. Odum. *Systems ecology: An introduction*. J. Wiley and Sons, 1983.
- H.T. Odum. *Environmental accounting: Emergy and environmental decision making*. J. Wiley and Sons, 1996.
- Ilya Prigogine and Isabelle Stengers. *Order out of chaos: Man's new dialogue with nature*. Bantam Books, 1984.
- A. H. Reis and A. Bejan. Constructal theory of global circulation and climate. *International Journal of Heat and Mass Transfer*, 49:1857–1875, 2006.
- V. M. Savage, J. F. Gillooly, W. H. Woodruff, G. B. West, A. P. Allen, B. J. Enquist, and J. H. Brown. The predominance of quarter-power scaling in biology. *Functional Ecology*, 18: 257–282, 2004.
- Knut Schmidt-Nielsen. *Scaling: Why is animal size so important?* Cambridge University Press, 1984.
- Knut Schmidt-Nielsen. *Animal Physiology: Adaptation and environment*. Cambridge University Press, 1997.
- Eric D. Schneider and James J. Kay. Complexity and thermodynamics: Towards a new ecology. *Futures*, 26:626–647, 1994.
- Dolph Schuler. Ecology and the origin of species. *Trends in Ecology & Evolution*, 16(7): 372–380, 2001.
- Enrico Sciubba and Sergio Ulgiati. Emergy and exergy analyses: complementary methods or irreducible ideological options? *Energy*, 30:1953–1988, 2005.
- R. M. Sibly and J. H. Brown. Effects of body size and lifestyle on evolution of mammal life histories. *Proceedings of the National Academy of Sciences of the United States of America*, 104:10900–10903, 2007.
- Tânia Sousa, Rui Mota, Tiago Domingos, and S. A. L. M. Kooijman. Thermodynamics of organisms in the context of dynamic energy budget theory. *Physical Review E*, 74:051901, 2006.



- Tânia Sousa, Tiago Domingos, and S. A. L. M. Kooijman. From empirical patterns to theory: A formal metabolic theory of life. *Philosophical Transactions of the Royal Society B*, 363: 2453–2564, 2008.
- W. Spirkel and H. Ries. Optimal finite-time endoreversible processes. *Physical Review E*, 52 (4):3485–3489, 1995.
- W. R. Stahl. Scaling of respiratory variables in mammals. *Journal of Applied Physiology*, 22 (3):453–460, 1967.
- Olivier Toussaint and Eric Schneider. The thermodynamics and evolution of complexity in biological systems. *Comparative Biochemistry and Physiology*, 120:3–9, 1998.
- Jaap van der Meer. Metabolic theories in ecology. *Trends in Ecology and Evolution*, 21(3): 136–140, 2006.
- L. von Bertalanffy. A quantitative theory of organic growth (inquiries on growth laws.ii). *Human Biology*, 10:181–213, 1938.
- G. B. West, W. H. Woodruff, and J. H. Brown. Allometric scaling of metabolic rate from molecules and mitochondria to cells and mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 99:2473–2478, 2002.
- Geoffrey West and James Brown. The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. *Journal of Experimental Biology*, 208:1575–1592, 2005.
- C. R. White and R. S. Seymour. Mammalian basal metabolic rate is proportional to body mass<sup>2/3</sup>. *Proceedings of the National Academy of Sciences of the United States of America*, 100:4046–4049, 2003.