Entropy production as a metabolic quantifier in intra- and inter-species comparisons

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The quantification of metabolic activity is usually done with mass or energy fluxes, e.g. dioxygen consumption or heat flux, that are not universal measures of metabolic activity. We propose the use of entropy production as a universal quantifier of metabolic activity, given its association with energy transformation, in order to unify the measurability and comparability of all types of metabolism.
However, entropy production is not directly measurable. We obtain it with the use of a general theory for organisms based on physical and chemical principles, the Dynamic Energy Budget theory, that provides quantification for biochemical activity at the individual level and across species.
In the literature the usual measures of metabolism – dioxygen flux and heat flux – are described by allometric rules. We compare DEB model results for entropy production and for those measures of metabolism with these rules.
Generally, entropy production is correlated with the dissipated heat flux once the entropy content of the net mass fluxes is negligible for the considered aerobic organism. Intra-specifically, entropy production is strongly affected by the initiation of assimilation at birth. Across related species, higher assimilation fluxes do not lead to proportionally higher maintenance costs, lowering the logarithmic slope of every variable, including entropy production. These particularities would be undistinguishable outside the used formal framework.

Metabolism | Dynamic Energy Budget | Entropy

Conceptually, metabolism is an aggregation of all reactions taking place within a given organism, unifying analysis for all types of organisms and the way they relate to mass and energy flows [1].

The problem of metabolic 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 plankton-sweeping dioxygen-using whale?

There have been two answers to this question: either quantify the scale of energy use as proportional a) to a mass flux, such as dioxygen [2], or b) to released heat via direct calorimetry [3]. Although useful, these measurements are not universal. The dioxygen flux is not a good measurement because many organisms do not use dioxygen consumptively. The heat flux is a misleading measurement for organisms that have both endothermic and exothermic chemical reactions because a given amount of heat dissipated cannot be linked unequivocally to a given set of chemical reactions [4]. In order to be universal, a given quantifier has to be applicable to all metabolisms and increase or decrease monotonically with the level of biochemical activity.

We propose the entropy production rate as a quantifier for metabolism. It is a universal measurement because all organisms are subject to the second law of thermodynamics, implying that all organisms produce entropy in their metabolic functioning and that this entropy production is always positive, being additive over all processes.

In order to quantify entropy production we use the Dynamic Energy Budget (DEB) theory and recent results obtained for the thermodynamics of organisms [5]. DEB theory is a biological non-species-specific theory that aims to capture the quantitative aspects of the organization of metabolism at the organism level. This theory presents disaggregated mass and energy fluxes as functions of model parameters and state variables [6]. Model parameters have to be obtained indirectly by statistically analyzing data [7] but gain mechanistic relevance within the theoretical structure that supports them. Hence, quantities such as the dioxygen flux, the dissipated heat flux and the entropy production can be mechanistically derived and explained. Another strong feature of this theory is that differences between species can be reduced to differences in parameter values that are roughly predicted by DEB theory to be a function of the species maximum size, allowing for inter-species comparisons according to that parameter.

We use the DEB model for an ectothermic animal to predict the intra- and inter-species dynamics of dioxygen flux, dissipated heat, and entropy production rate, and compare these results with descriptive allometric power rules.

Allometry

Statistical coherences of the distribution of general measurements with body mass M have led to the use of allometric relations, with the variable Y being assumed to follow $Y = Y_0(M/M_0)^\alpha$, where Y_0 and M_0 are normalization constants and α is the allometric power [2], although M_0 is usually ignored in allometric fittings.

In the literature, the dioxygen flux is considered to be the metabolic measurement for aerobic organisms. For this variable some allometric relations are proposed, yielding exponents of 3/4 [8, 9, 10], although values between 2/3 and 1 have also been found to fit data [11, 12, 13, 14]. Similarly, both dissipated heat flux [15] and entropy production rate [16] are argued to scale according to a 3/4 power law.

Several attempts have been made to explain these regularities. In the Metabolic Theory of Ecology, brought forth by Brown et al. [17], the explanation involves a minimization of transport costs in a infinitely fractally-branching space-filling closed network with invariant terminal branches and conserved cross-sectional area. However, this explanation suffers from several shortcomings. Only a very small fraction of organisms have a closed circulatory system, and dioxygen use

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is not ubiquitous. Van der Meer [18] discusses other inconsistencies of the MTE.

Dynamic Energy Budget theory

DEB theory, put forth by Kooijman [19], lays formal foundations for the chemical and physical principles of metabolism. At its simplest form, this theory can describe animal metabolic activity by abstracting an organism as separable units of structure, V, and reserve, E, that, according to a strong homeostasis assumption, have constant chemical compositions. Another basic assumption, weak homeostasis, is that given a constant level of feeding, organism chemical composition tends to a constant value, characteristic of the organism's species. Further theory explanations and extensions can be obtained in related literature [20, 21, 22].

In the DEB theory the difference between species is reduced to differences in parameter values and the relationship between parameters of different species is formalized, allowing for inter-species comparisons. Parameters are divided into two groups: primary parameters that describe internal cellular processes, similar for all scales, and design parameters, that are proportional to the maximum size of the species.

In this theory, energy from food enters the reserves by the assimilation process, $\dot{p}_A$, proportional to the surface of the organism, eventually leading to the excretion of products. Reserves fuel all processes via the mobilized power, $\dot{p}_C$, being a fixed κ 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 maturity development (in earlier stages) or reproduction (in the adult stage) $\dot{p}_R$. Allocation to somatic (maturity) maintenance takes precedence over growth (maturation or reproduction). These processes are represented in figure 1, where ovals are state variables and rectangles are metabolic activities.

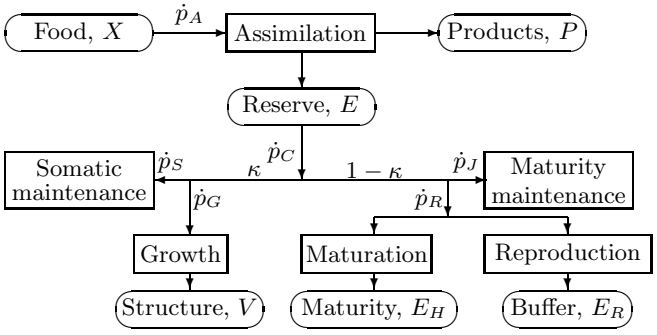

Fig. 1. Metabolic allocation schematics

This conceptualization leads to the reserve and structure dynamics presented in equation 1 that are used to model the organism's development.

$$\begin{cases} \frac{dE}{dt} = \dot{p}_A - \dot{p}_C \\ \frac{dV}{dt} = \frac{1}{[E_G]}\dot{p}_G \end{cases}, \qquad [1]$$

where $[E_G]$ is the constant parameter volume-specific cost of structure defined, as all other parameters, in table 2.[1]

In order to simplify the model, maturity E_H is assumed to be proportional to structural volume until adulthood and constant thereafter, which was found to be a reasonable approximation [23], removing maturity level as a state variable. Additionally, the reproductive buffer was considered to have negligible influence on the dynamics.

The model is implemented with constant feeding conditions in such a way that the reserve density $[E] = E/V$ is constant, therefore turning structure into the only variable of the model.

Processes presented in the scheme can be grouped according to general macro-chemical properties. While assimilation converts food into reserve plus products and growth converts reserve into structure, dissipation, $\dot{p}_D$, is defined as all reserve use towards purely informational purposes, such as maintenances and the inefficiencies of reproduction, as given by equation 2

$$\dot{p}_D = \dot{p}_S + \dot{p}_J + (1-\kappa_R)\dot{p}_R, \qquad [2]$$

where κ_R is the efficiency of the reproduction process, that is null except for the adult stage. The dissipation power rate accounts for all the "purposeful wasting" done in dissipative reactions with the exception of the overhead costs of assimilation and growth [21]. All power rates are computed according to the expressions presented in the Powers appendix. According to the presented definitions, assimilation is clearly proportional to organism surface area, defined as $V^{2/3}$, while the maintenance costs are mostly proportional to organism structural volume V, therefore making dissipation also proportional to structural volume.

In macrochemical terms, assimilation, dissipation and growth are aggregated as

$$\begin{cases} \dot{p}_A : X + Minerals \rightarrow E + P + Minerals \\ \dot{p}_D : E + Minerals \rightarrow Minerals \\ \dot{p}_G : E + Minerals \rightarrow V + Minerals \end{cases}, \qquad [3]$$

where the considered mineral compounds are CO_2, H_2O, O_2, and NH_3, as presented in the Compounds appendix. 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 [6]. 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, as shown in the Balances appendix. These quantities, after being obtained per unit of reserve produced or consumed, can be equated for the full metabolism by multiplication with the respective power rates. For example, the dioxygen consumption flux can be fully quantified as

$$\dot{J}_{O_2} = \begin{bmatrix} \eta_{O_2,A} & \eta_{O_2,D} & \eta_{O_2,G} \end{bmatrix} \begin{bmatrix} \dot{p}_A \\ \dot{p}_D \\ \dot{p}_G \end{bmatrix} = \boldsymbol{\eta}_{O_2}^T \dot{\boldsymbol{p}}, \qquad [4]$$

where η_{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

$$\dot{p}_{T+} = \begin{bmatrix} \xi_{T+,A} & \xi_{T+,D} & \xi_{T+,G} \end{bmatrix} \begin{bmatrix} \dot{p}_A \\ \dot{p}_D \\ \dot{p}_G \end{bmatrix} = \boldsymbol{\xi}_{T+}^T \dot{\boldsymbol{p}}, \qquad [5]$$

[1] Square brackets [] represent volume-specific variables while curly brackets {} represent surface-specific variables.

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 be obtained by making mass, energy, and entropy balances of the DEB organism, yielding

$$\dot{\sigma} = \begin{bmatrix} \gamma_A & \gamma_D & \gamma_G \end{bmatrix} \begin{bmatrix} \dot{p}_A \\ \dot{p}_D \\ \dot{p}_G \end{bmatrix} = \boldsymbol{\gamma}^T \dot{\boldsymbol{p}}, \qquad [6]$$

where γ_* 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, being presented in table 4, while $\dot{\boldsymbol{p}}$ is recursively obtained given feeding conditions and structural volume.

Inter-species analysis. Equations above are used for an individual defined by the dynamics of structure, reserve and maturity during its life cycle, according to the parameter set, i.e., for an intra-species comparisons. However, DEB theory also deals with the co-variation of parameter values across taxa, allowing for inter-species comparisons. While parameters that relate to the local metabolic environment in an individual are fixed, physical design parameters vary with maximum structural length, defined by $L_m = \kappa\{\dot{p}_{Am}\}/[\dot{p}_M]$.

Of the standard DEB model's primary parameters shown in table 2, only the maximum surface area-specific assimilation rate scales with maximum structural length and the threshold levels at birth and puberty scale with maximum structural volume, $V_m = L_m^3$. Hence, variables values can be compared across species taking into account these variations of maximum structure: different values of L_m beget different parameter values and consequently different results for the model.

The inter-species comparison is made for fully grown organisms with the reference species being defined by the presented parameter set. According to the assumed proportionality between maintenances, full access to food, and the fact that the inter-species comparison is made for fully grown organisms, reserve and maturity dynamics become proportional to maximum volume dynamics, simplifying the calculations.

Results

In this section, we use the standard DEB model to quantify entropy production (presented in the article), dioxygen flux, and dissipated heat (both presented in the Supporting Information) for a theoretical organism in intra- and inter-species comparisons. Notice that the behavior of these variables is presented in log-log scaling with organism wet weight, which expression is presented in the Wet weight appendix. We compare DEB results with the allometric rules presented in the literature to describe these metabolic quantifiers. The model is further particularized in the appendixes for ectothermic, isomorphic animals with total access to food.

Intra-species analysis. The dioxygen flux was found to scale approximately at a logarithmic slope of 0.84, mostly given the contribution of the dissipation power rate, that scales proportionally to V.

The dissipated heat flux approximately follows a 0.78 power law, once dissipation is not as important as it was for the dioxygen flux, i.e., its heat coupler value is not as high when compared with the other power rates as its dioxygen consumption coupler, as seen in table 4.

The scaling of entropy production is presented in figure 2.

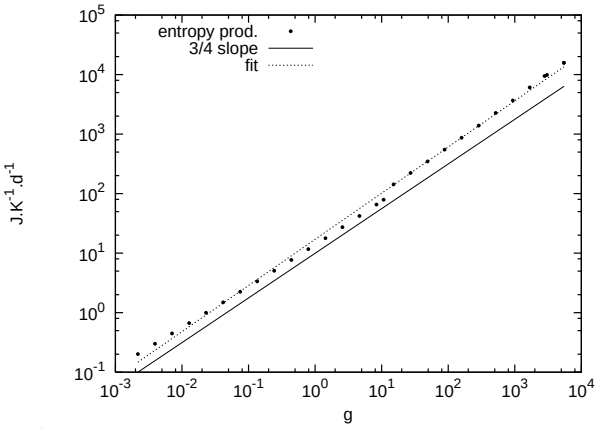

Fig. 2. Absolute entropy production vs. wet weight for the intra-species comparison

Entropy production follows a 0.78 power law, concurrently with $\dot{p}_{T+}$. This is motivated by the fact that the irreversibilities generated by aerobic reactions, $T\Delta s$, are negligible compared to the change in enthalpy, Δh [24], which simplifies the entropy balance of the organism to $T\dot{\sigma} \approx -\dot{p}_{T+}$. The presented discontinuity is registered at birth given the start of assimilation, that necessarily introduces a new positive contribution towards the total production of entropy of the organism, as seen in the Supporting Information.

Inter-species analysis. Across related species, the scaling of the dioxygen flux approximates a 0.85 power law, illustrating the relevance of maximum structure for internal energy dynamics. Concurrently, $\dot{p}_{T+}$ is approximated by power laws with the same exponent value, indicating equal relevance of the parameters for all the variables.

The absolute entropy production behavior with wet weight is presented in figure 3.

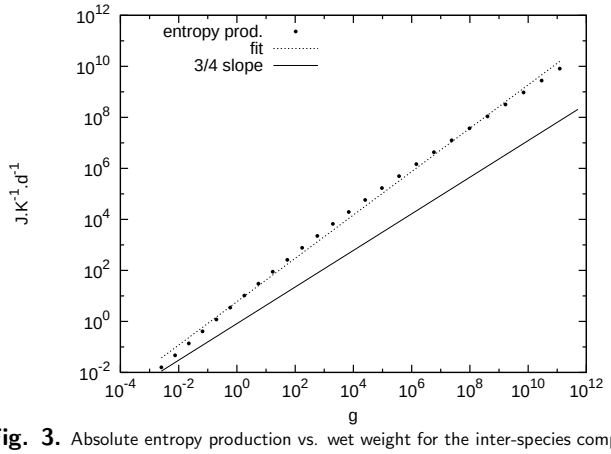

Fig. 3. Absolute entropy production vs. wet weight for the inter-species comparison

Absolute entropy production describes a behavior similar to those described by the other variables, approximated by 0.85 power laws, connecting their mechanistical backgrounds and indicating that all these processes are affected in the same way by changes in maximum volume.

However, these behaviors are not allometric, presenting the deviations clear in figure 3 for small species. In fact, these deviations are associated with the fact that the maximum reserve density, $[E_m] = \{\dot{p}_{Am}\}/\dot{v}$, scales with maximum length, given that energy conductance $\dot{v}$ is a constant parameter. For small species the reserve density is proportionally low, leading to high logarithmic slopes that, with the increase in maximum volume, tend to a lower value as can be seen in figure 3. This phenomenon is explained by taking into account that inter-species comparisons are based in fully grown organisms, hence completely characterized by $\dot{p}_A$ and $\dot{p}_D$.

As maximum structural volume increases, so do the parameters that determine the way in which the organisms uptake and establish reserves, while these higher reserve accomulations do not need maintenance, therefore pushing the slope toward lower values, away from the unitary slope, i.e., portionality to weight, of maintenance costs.

The fact that all metabolic rates approximately follow equivalent power laws point to a partial validation of allometry, but only for larger sizes. This could explain fitting power laws closer to 3/4, given an understandable bias toward data collection from larger species.

Sensitivity analysis. The presented results were subjected to tests for parameter sensitivity, by arbitrarily using different parameter values for $\dot{k}_M$, κ, l_p, and l_b, separately. These parameters were selected for their relevance in growth dynamics and the allocation of energy. Notice that these length stage thresholds are only valid if both somatic and maturity maintenance costs are proportional.

The obtained results for these runs generally maintained behaviors, especially so in the inter-species comparison, where all the exponents were constant. Such result points to the equivalence of energy processing in related species.

Concluding Remarks

By representing a property that is associated with any energy and mass transformation, entropy production is not limited by its applicability to any type of metabolism. However, it is limited by the availability of meaningful descriptions of the mechanisms involved, once it is not readily measurable in experimental procedures. Hence, entropy production has to be provided by formal mechanistic frameworks for metabolism such as DEB theory.

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

Also, the theoretical framework also allows the identification of the effects of stage transitions such as birth on metabolic activity. These models also allow distinctions that would otherwise have to be artificially introduced, such as the differences between comparing the same organism throughout its development and comparing different organisms from separate species. These are distinct analyzes because different species have different energy uptake and accumulation limits, determined by design parameters.

Entropy production scales similarly to the dissipated heat flux in organisms with similar chemical composition and metabolic activity. However, these results only hold if all biochemical reactions are exothermic, assuring the representativity of the dissipated heat flux as a metabolic quantifier [5].

Across related species, all analyzed variables are affected in the same way by the species maximum volume, reflecting the similar importance of reserve density to metabolic allocation of energy and associated production of entropy.

In conclusion, we show that entropy production has to be obtained in a mechanistic framework in order to properly represent metabolic activity and its relation to organism shape.

Appendix: Powers

According to model simplifications, scaled reserve density $e = [E]/[E_m]$ is constant, where $[E_m]$ is the maximum reserve density, a design parameter. Also notice that $V = L^3$, where L is a representative structural length of the organism and scaled length $l = L/L_m$, where L_m is the organism's species maximum length, given by $L_m = \kappa\{\dot{p}_{Am}\}/[\dot{p}_M]$, where κ is the referred allocation fraction, $\{\dot{p}_{Am}\}$ is the maximum surface area-specific assimilation rate, and $[\dot{p}_M]$ is the volume-specific somatic maintenance cost.

Assimilation power $\dot{p}_A$ represents all free energy "income" fixed into reserves from food. By definition $\dot{p}_A = f\{\dot{p}_{A_m}\}V^{2/3}$, where scaled functional response f is a measure of food availability, being in this model fixed at 1. Assimilation is made across surfaces that, in the particular case of isomorphy, represent a fixed part of total surface area.

The catabolic power is obtained from the reserve dynamics in the organism [6], yielding

$$\dot{p}_C = E\frac{\frac{[E_G]}{[E_m]}\frac{\{\dot{p}_{A_m}\}}{V^{1/3}} + [\dot{p}_M]}{\kappa[E] + [E_G]}, \qquad [7]$$

Somatic maintenance is defined as $\dot{p}_S = [\dot{p}_M]V$.

Maturity maintenance $\dot{p}_J$ is proportional to maturity level E_H, which can be considered proportional to structure in this simplified model. Hence, $\dot{p}_J = \frac{1-\kappa}{\kappa}[\dot{p}_M]\min\{V, V_p\}$, where V_p is the structural volume at puberty.

Growth is defined as the increase in structure [6], and as such the power allocated to growth is

$$\dot{p}_G = [E_G]\frac{dV}{dt}, \text{ with } \frac{dV}{dt} = \kappa\{\dot{p}_{A_m}\}\frac{e-l}{\kappa[E_m] + [E_G]}L^2. \qquad [8]$$

Finally, energy allocated to maturation or reproduction $\dot{p}_R$ is the $1-\kappa$ part of $\dot{p}_C$ that is not used in maturity maintenance, effectively

$$\dot{p}_R = (1-\kappa)\dot{p}_C - \frac{1-\kappa}{\kappa}[\dot{p}_M]\min\{V, V_p\}. \qquad [9]$$

The expressions used for the several power fluxes in DEB are presented in table 3 both for the intra-species and the inter-species analyzes, where $g = [E_G]/\kappa[E_m]$ represents the energy investment ratio. The inter-species expressions are obtained from the intra-species adult expressions using full growth, full access to food, where only the adimensionalizing power rate $\{\dot{p}_{Am}\}L_m^2$ changes, pointing to the power of the simplifications made for the inter-species analysis.

Appendix: Compounds

In the used model the mineral compounds are CO_2, H_2O, O_2 and NH_3, and the organic compounds are food

X ($CH_{1.8}O_{0.5}N_{0.2}$), structure V ($CH_{1.8}O_{0.5}N_{0.15}$), reserve E ($CH_2O_{0.75}N_{0.2}$) and products, primarily excretions P ($CH_{1.8}O_{0.5}N_{0.15}$). The thermodynamic properties of these compounds are presented in table 1.

Entropy and enthalpy vectors for compound group $*$ are respectively $\overline{s}_*$ and $\overline{h}_*$, 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* [25] for mineral compounds. Formation enthalpy values for X and P where computed using Thornton's coefficient of -444 kJ/mol of O_2 and the entropies where computed using an empirical rule proposed by Battley [26]. Formation enthalpies and entropies for E and V were obtained from a work by Sousa et al. [5].

Appendix: Wet weight

The wet weight expressions are obtainable simply by adding structure and reserve weight contributions. Hence, wet weight for intra-species is equal to

$$W_w = \left(d_V + [E]\,\frac{w_E}{\mu_E}\right) V, \qquad [10]$$

where d_V represents structure density, w_E reserve molar weight, and μ_E the reserve's chemical potential. The interspecies expression for wet weight is

$$W_w^{(e)} = \left(d_V + \frac{L_m}{L_m^{REF}}\,[E_m]\,\frac{w_E}{\mu_E}\right) V_m, \qquad [11]$$

where $L_m^{REF} = \kappa\{\dot{p}_{Am}\}/[\dot{p}_M]$ is the reference species' maximum volume, given by the presented values of these parameters, and L_m is the true variable in the interspecies comparison.

Appendix: Balances

Mass, energy, and entropy balances for the assimilation, dissipation, and growth macro-chemical reactions, are used to obtain the couplers needed to quantify the respective contributions to dioxygen flux, dissipated heat flux, and entropy production rate. For extension sake, the method will only be applied to the assimilation reaction.

The assimilation reaction is presented in equation 12 after its stoichiometry has been adjusted to observe mass conservation for all chemical elements.

$$X + 0.06H_2O + 0.1O_2 \rightarrow 0,75E + 0,2P + 0.05CO_2 + 0.02NH_3 \qquad [12]$$

By making energy and entropy balances to this reaction, the contributions to dissipated heat and entropy productions are respectively obtained by

$$q_{\dot{p}_{T+},A} + \sum n_{i,A}\overline{h}_{i,A} = 0 \qquad [13]$$

and

$$q_{\dot{\sigma},A} + \frac{q_{\dot{p}_{T+},A}}{T} + \sum n_{i,A}\overline{s}_{i,A} = 0, \qquad [14]$$

where i, A represents each of the chemical compounds involved in the assimilation reaction, according to the presented molar enthalpy and molar entropy values for the compounds and their stoichiometry, and imposing positive stoichiometric coefficients n_* for the reagents and negative n_* for the products. The contributions $q_{\dot{p}_{T+},A}$ and $q_{\dot{\sigma},A}$ are then converted into a reserve unit basis instead of a reaction basis by division by $\mu_E n_E$, the amount of reserve converted for each reaction, yielding

$$\begin{cases} \eta_{O_2,A} = \frac{n_{O_2,A}}{\mu_E n_{E,A}} \\ \xi_{T+,A} = \frac{q_{\dot{p}_{T+},A}}{\mu_E n_{E,A}} \\ \gamma_A = \frac{q_{\dot{\sigma},A}}{\mu_E n_{E,A}} \end{cases} . \qquad [15]$$

The process for obtaining couplers for oxygen flux, dissipation and growth is perfectly analogous to the one presented for assimilation. The obtained coupler values are presented in table 4, where the overall importance of the dissipation process for all fluxes is clear in comparison with the other two.

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Table 1. Flux entropy and enthalpy values

	$\overline{\boldsymbol{s}}_{\mathcal{M}}$ $[JK^{-1}]$	$\overline{\boldsymbol{h}}_{\mathcal{M}}$ $[J]$		$\overline{\boldsymbol{s}}_{\mathcal{O}}$ $[J.K^{-1}.mol^{-1}]$	$\overline{\boldsymbol{h}}_{\mathcal{O}}$ $[J.mol^{-1}]$
CO_2	$\begin{bmatrix} 213.47 \end{bmatrix}$	$\begin{bmatrix} -3.93 \times 10^5 \end{bmatrix}$	X	$\begin{bmatrix} 36.00 \end{bmatrix}$	$\begin{bmatrix} -1.17 \times 10^5 \end{bmatrix}$
H_2O	$\begin{bmatrix} 69.84 \end{bmatrix}$	$\begin{bmatrix} -2.86 \times 10^5 \end{bmatrix}$	V	$\begin{bmatrix} 52.00 \end{bmatrix}$	$\begin{bmatrix} -1.07 \times 10^5 \end{bmatrix}$
O_2	$\begin{bmatrix} 204.83 \end{bmatrix}$	$\begin{bmatrix} 0 \end{bmatrix}$	E	$\begin{bmatrix} 74.80 \end{bmatrix}$	$\begin{bmatrix} -3.30 \times 10^4 \end{bmatrix}$
NH_3	$\begin{bmatrix} 111.18 \end{bmatrix}$	$\begin{bmatrix} -8.01 \times 10^4 \end{bmatrix}$	P	$\begin{bmatrix} 35.00 \end{bmatrix}$	$\begin{bmatrix} -1.17 \times 10^5 \end{bmatrix}$

Table 2. Parameter description for an animal isomorph in DEB. Parameters l_b, l_p are educated guesses, all other values were obtained from DEBtool

Par	Description	Value	Units
$\{\dot{p}_{A_m}\}$	Max. spec. assimilation power	11.6	kJ.cm^{-2}d^{-1}
$\dot{v}$	Energy conductance	1.0	cm.d^{-1}
κ	Allocation fraction to soma	0.8	–
κ_R	Reproduction efficiency	0.8	–
$[\dot{p}_M]$	Volume-spec. som. maint. cost	0.68	kJ.d^{-1}cm^{-3}
$\{\dot{p}_T\}$	Surface-spec. temperature maint. cost	0	kJ.d^{-1}cm^{-2}
$\dot{k}_M = \dot{k}_J$	Maintenance rate coefficient	0.05	d^{-1}
$[E_G]$	Volume-specific cost for structure	13.6	kJ.cm^{-3}
l_b	Scaled length at birth	0.125	–
l_p	Scaled length at puberty	0.8	–
T	Temperature	293	K
μ_E	Reserve's chemical potential	283.3	kJ.mol^{-1}
w_E	Reserve molar weight	28.8	g.mol^{-1}
d_V	Structure density	1.0	g.cm^{-3}
y_{EX}	Reserve to food coupler	0.75	mol.mol^{-1}
y_{PX}	Product to food coupler	0.20	mol.mol^{-1}
y_{EV}	Reserve to structure coupler	1.15	mol.mol^{-1}

Table 3. Power rate expressions for the modeled 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	$el^2\frac{g+l}{g+e}$	$el^2\frac{g+l}{g+e}$	$el^2\frac{g+l}{g+e}$	1
S	κl^3	κl^3	κl^3	κ
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	$(1-\kappa)\,l^2\frac{e-l}{1+e/g}$	$(1-\kappa)\,l^2\frac{e-l}{1+e/g}$	$(1-\kappa)\left(l^2\frac{e-l}{1+e/g}+l^3-l_p^3\right)$	$(1-\kappa)\left(1-l_p^3\right)$

Table 4. Dioxygen, dissipated heat, and entropy production couplers for the assimilation, dissipation, and growth processes.

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