7. APPENDICES

A. Appendix I

Proof. (Proposition 3.7)

It follows from Eq. 3.6 and Eq. 3.10. $\qquad\square$

Proof. (Proposition 3.8)

Empirical evidence shows that eggs use dioxygen (R2) but freshly laid eggs do not (R1). Thus, there are metabolic processes occurring during the embryo stage that are not present at the beggining (fresh laid egg). The energy used in all metabolic processes comes from reserves (Assumption 3.4) implying that eggs must have reserve. However, reserve is not produced during the embryo stage because the organism does not feed (Assumptions 3.2 and 3.4), i.,e., freshly laid eggs must have reserve. Also, freshly laid eggs can not have a significant amount of structure because they do not pay maintenance (Assumption 3.5). Thus, freshly laid eggs are composed of reserve only. $\qquad\square$

Proof. (Proposition 3.9)

The $z + 2$ stoichiometric coefficients a_1 to a_z, b_1 and b_2 of the assimilation process (Eq. 3.13) are completely determined if we have at least $z + 2$ chemical elements because each chemical element must obey a mass balance and the chemical composition of food, faeces (a product) and reserve are constant (Assumption 3.3). The same reasoning applies to the growth and dissipation processes. The yield coefficients η_{*1*2} are constant because they are only dependent on y_{*1*2} and thermodynamic properties that are constant (Assumption 3.3), e.g., $\eta_{XA} = 1/(y_{EX}^A \mu_E)$.

$\qquad\square$

Proof. (Proposition 3.10)

The net flows (input-output) at the boundary of the organism, are given by:

$$\dot{J}_{*1} = \dot{J}_{*1A} + \dot{J}_{*1D} + \dot{J}_{*1G} \tag{7.1}$$

where $*1$ stands for CO_2, O_2, heat, N_{waste}, H_2O and other compounds, $\dot{J}_{*1A}$, $\dot{J}_{*1G}$ and $\dot{J}_{*1D}$ are the net flows of $*1$ in the assimilation, growth and dissipation processes, respectively. Eq. 7.1 can be rewritten as:

$$\dot{J}_{*1} = \eta_{*1A}\dot{p}_A + \eta_{*1D}\dot{p}_D + \eta_{*1G}\dot{p}_G \tag{7.2}$$

where $\dot{J}_{*1A} \equiv \eta_{*1A}\dot{p}_A$, $\dot{J}_{*1G} \equiv \eta_{*1G}\dot{p}_G$ and $\dot{J}_{*1D} \equiv \eta_{*1D}\dot{p}_D$ (definition of η_{*1*2} in Proposition 3.9).

To obtain $\dot{p}_A$, $\dot{p}_D$ and $\dot{p}_G$ we have to: 1) know the net flows of any 3 compounds, 2) apply Eq. 7.2 for each compound to obtain

$$
\begin{bmatrix} \dot{J}_{*2} \\ \dot{J}_{*3} \\ \dot{J}_{*4} \end{bmatrix} = \begin{bmatrix} \eta_{*2A} & \eta_{*2D} & \eta_{*2G} \\ \eta_{*3A} & \eta_{*3D} & \eta_{*3G} \\ \eta_{*4A} & \eta_{*4D} & \eta_{*4G} \end{bmatrix} \begin{bmatrix} \dot{p}_A \\ \dot{p}_D \\ \dot{p}_G \end{bmatrix} ;
\tag{7.3}
$$

and 3) invert the square matrix in Eq. 7.3. This matrix is invertible if the columns are linearly independent. This occurs because 1) each column is the set of conversion factors associated with each metabolic process, 2) each set is dependent on the stoichiometry of the aggregate chemical reaction that describes that process and 3) growth, dissipation and assimilation correspond to different aggregate chemical reactions.

Each power is a weighted average of the flows of 3 compounds. Thus, the flow of compound $*1$ (Eq. 7.2) can be written as a weighted average of any 3 compounds $\dot{J}_{*2}$, $\dot{J}_{*3}$ and $\dot{J}_{*4}$. $\qquad\square$

Proof. (Proposition 3.12)

By replacing $\dot{J}_X$ in Eq. 3.16 with

$$
\dot{J}_X = \eta_{XA}\dot{p}_A,
\tag{7.4}
$$

it follows that

$$
\dot{p}_A = \frac{\{\dot{J}_{Xm}\}}{\eta_{XA}}V^{2/3}f(X).
\tag{7.5}
$$

Proposition 3.9 implies that η_{XA} is constant and therefore $\{\dot{p}_{Am}\} \equiv \frac{\{\dot{J}_{Xm}\}}{\eta_{XA}}$ is also constant. $\qquad\square$

Proof. (Proposition 3.13)

Each different category of chemical compounds, E_i, must represent a constant fraction λ_i of the aggregate reserve E, otherwise the chemical composition of reserve as a whole would change, violating Assumption 3.3.

The catabolic power mobilized from E_i has the chemical composition of that category of compounds. Therefore, the mobilization of the different categories of chemical compounds, E_i, must be coordinated, such that the aggregate chemical composition of the catabolic power is the same as the chemical composition of E (Assumption 3.4) implying that $\dot{p}_{Ci} = \lambda_i\dot{p}_C$.

Also, the allocation to growth and maintenance of the different categories of chemical compounds, E_i, must be coordinated, such that the aggregate chemical composition of the catabolic

power allocated to these metabolic processes is the same as E's (see the chemical composition of $\dot{p}_G$ and $\dot{p}_M$ in Assumption 3.4),

$$\kappa_i \dot{p}_{Ci} = \lambda_i \kappa \dot{p}_C. \tag{7.6}$$

Equation 7.6 implies that $\kappa_i = \kappa$. The same reasoning applies to the other energy flows. Again, the catabolic power mobilized from each category E_i to 1) maintenance and growth, 2) maintenance and 3) growth is proportional to the amount of energy embodied in it, i.e.,

$$\dot{p}_{Mi} = \lambda_i \dot{p}_M; \quad \dot{p}_{Gi} = \lambda_i \dot{p}_G. \tag{7.7}$$

Equations 3.8, 3.3 and 7.7 imply that $[\dot{p}_{Mi}]^* = \lambda_i [\dot{p}_M]^*$ and $[E_{Gi}] = \lambda_i [E_G]$. The relationship between the overall metabolic power and the metabolic power mobilized from each category is the following:

$$\dot{p}_{Ci}(E_i, V, [\dot{p}_{Mi}]^*, [E_{Gi}], \kappa_i) = \lambda_i \dot{p}_C(E, V, [\dot{p}_M]^*, [E_G], \kappa). \tag{7.8}$$

This equation can written as Eq. 3.20 using Eq. 7.7 and $\kappa_i = \kappa$.

The assimilation power that goes to E_i has the chemical composition of that category of compounds. Therefore, the assimilation power that goes to the different categories of chemical compounds, E_i, must be coordinated, such that the aggregate chemical composition of the assimilation power is the same as the chemical composition of E (Assumption 3.4) implying that $\dot{p}_{Ai} = \lambda_i \dot{p}_A$. Thus, the reserve dynamics of each category of chemical compounds is:

$$\frac{d}{dt} E_i = \dot{p}_{Ai} - \dot{p}_{Ci} = \lambda_i (\dot{p}_A - \dot{p}_C). \tag{7.9}$$

Eq. 3.19 is obtained with Eq. 7.9. $\qquad\square$

Proof. (Proposition 3.14)

Follows from Eq. 3.20 and 7.6. $\qquad\square$

Proof. (Proposition 3.16)

Maintenance powers, $\dot{p}_M$ and $\dot{p}_J$ given by Eq. 3.8 and Eq. 3.10 are set by the state of the organism V, by κ and other parameters that are constant. The energy that is not needed for maintenance purposes is then allocated to growth by Eq. 3.3 and to maturation or reproduction by Eq. 3.11 or Eq. 3.12. $\qquad\square$

Proof. (Proposition 3.18)

By the definition of reserve density:

$$\frac{d[E]}{dt} = \frac{1}{V}\frac{dE}{dt} - [E]\dot{r}. \tag{7.10}$$

Using Eq. 3.2 to replace $\frac{dE}{dt}$ and then Eq. 3.18 to replace $\dot{p}_A$, Eq. 7.10 becomes:

$$\frac{d[E]}{dt} = \{\dot{p}_{Am}\}V^{-1/3}f(X) - [\dot{p}_C] - [E]\dot{r}. \tag{7.11}$$

This can be written as

$$\frac{d[E]}{dt} = \{\dot{p}_{Am}\}V^{-1/3}f(X) - \Phi(V,[E]), \tag{7.12}$$

because 1) $\dot{p}_C$ is a function of E and V (see Assumption 3.4), 2) dV/dt is proportional to $\dot{p}_G$ (see Eq. 3.3) and 3) $\dot{p}_G$ is a function of E and V (see Assumption 3.4).

Assumption 3.17 implies that for any constant food level there is a reserve density $[E]^*$ that remains constant, i.e., $\frac{d[E]}{dt} = 0$. For $[E]^*$ Eq. 7.12 simplifies to

$$\{\dot{p}_{Am}\}V^{-1/3}f(X) = \Phi(V,[E]^*). \tag{7.13}$$

Also, Assumption 3.17 says that $[E^*]$ is independent of volume because it remains constant along the growth process, implying that $\Phi(V,[E]^*) = V^{-1/3}H([E]^*)$.

Function $\Phi(V,[E])$ can be generalized out of steady-state as $\Phi(V,[E]) = V^{-1/3}H([E]) + ([E^*] - [E])G(V,[E],X^*)$ imposing that $\frac{d}{dX}\left(([E^*] - [E])G(V,[E],X)\right) = 0$ because $\Phi(V,[E])$ does not depend on food. Condition $\frac{d}{dX} = 0$ implies that $G(V,[E],X) = A\frac{1}{[E^*]-[E]}$ where A is a constant, i.e., $([E^*] - [E])G(V,[E],X^*) = A$.

Using this expression, Eq. 7.11 and Eq. 7.12, the catabolic flux can be written as

$$[\dot{p}_C] = V^{-1/3}H([E]) + A - [E]\dot{r}, \tag{7.14}$$

or

$$\dot{p}_C = V^{2/3}H([E]) + AV - [E]V\dot{r}. \tag{7.15}$$

The condition $\dot{p}_C = 0$ when the amount of reserve is null implies that $A = 0$. Proposition 3.13 on the partitionability of reserve dynamics is used to further specify $H([E])$. In the case of a fully grown adult ($dV/dt = 0$), Eq. 3.20 implies that

$$\lambda H([E]) = H(\lambda[E]). \tag{7.16}$$

Therefore $H([E]) = \dot{v}[E]$ where $\dot{v}$ is a parameter, the energy conductance, and Eq. 7.14 simplifies to:

$$[\dot{p}_C] = \dot{v}[E]V^{-1/3} - [E]\dot{r}. \tag{7.17}$$

$\square$

Proof. (Proposition 3.19)

With Eq. 7.17 the reserve density dynamics given by Eq. 7.11 is simplified to:

$$\frac{d[E]}{dt} = V^{-1/3}\left(\{\dot{p}_{Am}\}f(X) - \dot{v}[E]\right). \tag{7.18}$$

At any constant food level $\frac{d[E]}{dt} = 0$ (Assumption 3.17) implying that $[E^*] = \frac{\{\dot{p}_{Am}\}f(X)}{\dot{v}}$. At abundant food, $f_X = 1$ (Assumption 3.11), implying that $[E_m] = \frac{\{\dot{p}_{Am}\}}{\dot{v}}$. Since $\{\dot{p}_{Am}\}$ and $\dot{v}$ are finite parameters $[E_m] < \infty$. $\square$

Proof. (Proposition 3.20)

Replacing $\dot{p}_G$ in Eq. 3.3 by Eq. 3.5, 2) replacing $\dot{p}_C$ with Eq. 3.22 multiplied by V, 3) replacing $\dot{p}_M$ with Eq. 3.8 and 4) replacing V with L^3, the following is obtained:

$$\frac{dL}{dt} = \frac{1}{3}\frac{[E]\dot{v}\kappa - [\dot{p}_M]L - \{\dot{p}_T\}}{[E_G] + \kappa[E]}. \tag{7.19}$$

When the food level is maximum, i.e., $E = E_m$ (Assumption 3.17), the organism grows until it reaches the following length:

$$L = \frac{\kappa\{\dot{p}_{Am}\}}{[\dot{p}_M]} - \frac{\{\dot{p}_T\}}{[\dot{p}_M]}. \tag{7.20}$$

where $[E_m]$ has been replaced by Eq. 3.24. The maximum length L_m is achieved when the surface maintenance costs are null, i.e., $L_m = \frac{\kappa\{\dot{p}_{Am}\}}{[\dot{p}_M]}$. $\square$

Proof. (Proposition 3.21)

Eq. 7.18 simplifies to

$$[E^*] = \frac{f(x)\{\dot{p}_{Am}\}}{\dot{v}} \tag{7.21}$$

at constant food level (Assumption 3.17). Eq. 3.26 is obtained inserting the expression for the maximum reserve density (Eq. 3.24). $\square$

Proof. (Proposition 3.23)

Eq. 3.27 is obtained by (1) multiplying Eq. 7.18 by $[E_m]$, (2) using the definition of scaled reserve density and (3) using the expression for maximum reserve density (Eq. 3.24). Eq. 3.28 is derived from Eq. 7.19 using Eq. 3.24, 3.25 and 3.29 and the definition of heating length L_h. $\square$

Proof. (Proposition 3.24)

If resource density is constant, X^*, scaled reserve density is $e^* = [E^*]/[E_m] = f(X^*)$ through most of the individual's life (see Eq. 3.26). Hence, the growth curve (see Eq. 3.28) is:

$$\frac{dL}{dt} = \frac{\dot{v}}{3}\frac{f - L_h/L_m - L/L_m}{g + f}. \tag{7.22}$$

Eq. 3.31 is obtained by combining Eq. 7.22 with Eq. 3.30 and Eq. 3.32. $\qquad\square$

Proof. (Proposition 3.25)

Eq. 3.33 is obtained by taking the limit $e \to \infty$ in the right hand side of Eq. 3.28. $\qquad\square$

Proof. (Proposition 3.26)

For organisms kept under fasting conditions

$$\dot{J}_{O_2} = \eta_{OD}\dot{p}_M + \eta_{OD}\dot{p}_J + (1 - \kappa_R)\eta_{OD}\dot{p}_R + \eta_{OG}\dot{p}_G, \tag{7.23}$$

where η_{OD} and η_{OG} are constant (Prop. 3.9).

Eq. 7.23 can be simplified to:

$$\dot{J}_{O_2} = \eta_{OD}\frac{1 - \kappa_R + \kappa_R\kappa}{\kappa}(\dot{p}_M + \dot{p}_G) + \eta_{OD}\kappa_R\dot{p}_J \tag{7.24}$$

by first inserting the expression for $\dot{p}_R$ given by Eq. 3.6 and then replacing $\dot{p}_C$ with Eq. 3.5.

The somatic and maturity maintenance powers are given by Eq. 3.8 and 3.10 and,

$$\dot{p}_G = [E_G]\dot{v}\frac{(e - L_h/L_m)V^{2/3} - V/L_m}{g + e}, \tag{7.25}$$

is obtained by combining Eq. 3.3 with Eq. 3.28. The power $\dot{p}_J$ is proportional to V while $\dot{p}_G$ and $\dot{p}_M$ are a linear combination of $V^{2/3}$ and V. The dioxygen consumption must be approximately proportional to V^α with $\alpha \in [2/3, 1]$ because it is a linear combination of $V^{2/3}$ and V (see below). If the animals of the same species have a similar reserve density then the proportionality constant between $\dot{J}_{O_2}$ and w^α is the same (see Eq. 7.36). $\qquad\square$

Suppose that we want make the following approximation for a polynomial

$$ax^{2/3} + bx \approx cx^\alpha, \tag{7.26}$$

in a given interval $[x^-, x^+]$, where $a > 0$, $b > 0$ and $c > 0$ are constants. In this case, we will choose α and c such that the total approximation error $\int_{x^-}^{x^+}(y(x, \alpha)x^\alpha - cx^\alpha)^2 dx$ where $y(x, \alpha) = ax^{2/3-\alpha} + bx^{1-\alpha}$ is as small as possible.

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To minimize the total error we impose that 1) there is a point x^* within the interval $[x^-, x^+]$ such that the error is null, i.e.,

$$c = ax^{*2/3-\alpha} + bx^{*1-\alpha}, \tag{7.27}$$

and that 2) at x^* the change with x is null, i.e.,

$$\left(\frac{\partial \left(y(x, \alpha)x^\alpha - cx^\alpha \right)}{\partial x} \right)_{x=x^*} = (2/3 - \alpha) ax^{-1/3} + (1 - \alpha)b = 0, \tag{7.28}$$

or that

$$\alpha = 1 - \frac{1}{3} \frac{ax^{-1/3}}{ax^{-1/3} + b}. \tag{7.29}$$

The optimal value for α is within the interval $[2/3, 1]$ because $0 < \frac{ax^{-1/3}}{ax^{-1/3}+b} < 1$. The optimal value for c is within the interval given by Eq. 7.27 for $\alpha \in [2/3, 1]$ and $x^* \in [x^-, x^+]$.

Proof. Proposition 4.3

Suppose that a reference species and species A are related and that $z = \frac{L_m^A}{L_m}$.

Parameter $\{\dot{p}_{Am}\}$ is proportional to L_m (see Eq. 3.25) because $\kappa = \kappa^A$ and $[\dot{p}_M] = [\dot{p}_M^A]$:

$$z = \frac{L_m^A}{L_m} = \frac{\{\dot{p}_{Am}^A\}}{\{\dot{p}_{Am}\}}. \tag{7.30}$$

□

Proof. Proposition 4.4

Suppose that a reference species and species A are related and that $z = \frac{L_m^A}{L_m}$.

Parameter L_h does not depend on L_m because both $\{\dot{p}_T\}$ and $[\dot{p}_M]$ are constant parameters and $L_h = \frac{\{\dot{p}_T\}}{[\dot{p}_M]}$.

Parameter $[E_m]$ is proportional to L_m, i.e., $[E_m^A] = z[E_m]$ because $\dot{v} = \dot{v}^A$ and $\{\dot{p}_{Am}^A\} = z\{\dot{p}_{Am}\}$ (see Eq. 3.24).

Parameter g is proportional to $\frac{1}{L_m}$, i.e., $g = zg^A$ because $[E_G] = [E_G]^A$, $\kappa = \kappa^A$ and $[E_m^A] = z[E_m]$ (see Eq. 3.29).

At abundant food (see Eq. 3.32), i.e., $f = 1$,

$$\dot{r}_B^A = \frac{\dot{v}^A}{3L_m^A} \frac{1}{g^A + 1}. \tag{7.31}$$

Eq. 4.1 is obtained by (1) rewriting the parameters of species A as a function of the parameters of the reference species and then (2) applying logarithms.

For fully grown organisms kept under fasting condition

$$\dot{J}_{O_2} = \eta_{OD}(\dot{p}_M + \dot{p}_J + (1 - \kappa_R)\dot{p}_R), \tag{7.32}$$

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where η_{OD} is constant (Prop. 3.9).

Eq. 7.32 can be simplified to Eq. 7.24 with $\dot{p}_G = 0$ by first inserting the expression for $\dot{p}_R$ given by Eq. 3.6 and then replacing $\dot{p}_C$ with Eq. 3.5.

For fully grown adults ($l = 1$ and $E_H = E_H^p$):

$$\dot{p}_M = \left([\dot{p}_M] + \frac{\{\dot{p}_T\}}{V_m^{A1/3}}\right) V_m^A, \tag{7.33}$$

$$\dot{p}_J = \dot{k}_J[E_H^p]V_m^A, \tag{7.34}$$

where all parameters are for the reference species with the exception of V_m^A. Eq. 7.33 to 7.34 were obtained from Eq. 3.8 and 3.10 respectively, by first replacing V with V_m because $l = 1$ and then rewriting the parameters of species A, as a function of the parameters of a reference species with the exception of V_m^A.

The power $\dot{p}_J$ is proportional to V_m^A while $\dot{p}_M$ is proportional to a linear combination of V_m^A and $V_m^{A\,2/3}$. The dioxygen consumption must be approximately proportional to $V_m^{A\alpha}$ with $\alpha \in [2/3, 1]$ because it is a linear combination of $V_m^{A\,2/3}$ and V_m^A.

The relationship between the weight and the volume of species A,

$$w = \frac{[E_m]e}{\mu_E V_m^{1/3}} V_m^{A\,4/3} + d_V V_m^A, \tag{7.35}$$

is obtained from Eq. 7.36 by replacing V with V_m, $[E]$ with $[E_m]e$ and rewriting the parameters of species A as a function of the parameters of a reference species with the exception of V_m^A. Thus, (1) the mass is approximately proportional to V_m^β with $\beta \in [1, 4/3]$ and (2) the dioxygen consumption is approximately proportional to $w^{\alpha/\beta}$ with $\alpha/\beta \in [0.5, 1]$. $\square$

B. Appendix II

The structural volume can be converted to weight using the following auxiliary proposition.

Proposition 7.1 (Volume to weight). *The relationship between weight, w, and structural volume, V, is*

$$w = \left(\frac{[E]}{\mu_E} + d_V\right) V = \left(\frac{[E_m]}{\mu_E}e + d_V\right) V, \tag{7.36}$$

where d_V is the density of the structure and μ_E is the chemical potential of reserve.

Proof. The volume of the organism can be written as,

$$\frac{[E]V}{d_E\mu_E} + V, \tag{7.37}$$

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where the first term is the volume of the reserve, i.e., the ratio between the reserve's energy, $[E]V$, and the reserve's energy per unit volume of reserve, $d_E \mu_E$, and d_E is the density of the reserve. The weight of the organism (Eq. 7.36) is obtained by multiplying the volume of the reserve by d_E and the volume of the structure by d_V. □