## Thermodynamics of Heterotrophic Organisms in the DEB theory

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In Dynamic Energy Budget (DEB) theory some conclusions are drawn for organisms based on a thermodynamic analysis for which the assumptions are not fully explicit [1]. In the present work we formalise and extend this thermodynamics analysis for heterotrophic organisms, making explicit which are the assumptions made in [1]. The formalisation presented follows the open systems thermodynamics analysis presented in [3].

The thermodynamic system, a heterotrophic organism, is defined according to the DEB theory [1]. A schematisation of the DEB theory (Figure 1) was undertaken to make explicit the incoming and outgoing fluxes through the outer surface of the organism, which according to [1] can be divided in organic - food, X, and faeces, P - and mineral compounds -  $O_2$ , nitrogenous waste,  $CO_2$  and water. In Figure 1 internal processes are also made explicit to get some insight into internal entropy production. The stars in Figure 1 are idealised reactors.

We obtain the energy balance equation presented in [1] by applying an energy balance equation to the set of reactors. The assumptions made are: reactors are at steady-state with negligible mass and no work transfer; total heat of reaction is equal to the total heat fluxes between the organism and its environment and the change in enthalpy,  $\Delta h$ , is equal to the change in Gibbs free energy,  $\Delta g$ . The last assumption stated is based on the empirical knowledge, stated in [2], that for some of the most important reactions in biological systems the term  $T \Delta s$  (temperature times change in entropy) is very small compared to  $\Delta h$ . This assumption is weaker than the one presented in [1] that: 'the entropy can safely be set to zero, which implies that enthalpies can be substituted for free energies'; because it applies only to reactions leaving out, for example, structure.

We also obtained the energy balance equation for the whole organism. The assumptions made are: the work is null in accordance with [1] that states that

work can be accounted for a reduction in assimilation efficiency; the heat is the heat exchanged by the organism with its surroundings and the enthalpy is equal to the internal energy. The last assumption is based on [2], that considers that 'the product pv (pressure times specific volume) is generally very small in comparison with the enthalpy of formation for compounds in biological systems'.

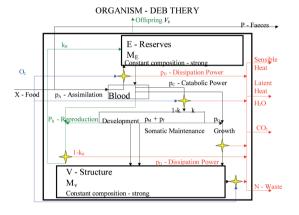


Figure 1: Schematisation of a heterotrophic organism following DEB theory.

We obtained an expression for the internal irreversibilities term  $T\sigma$ , based on both energy balance equations and on the entropy balance equation made by us for the whole organism, where internal irreversibilities are specified only by the net fluxes of chemical compounds in and out of the organism. Internal irreversibilities are also proved to be equal to the total heat released in the reactions inside the organism, proving that the total heat released is positive but failing to prove the stronger result presented in [1] that each of 'the processes of assimilation, dissipation and growth are exothermic'. We also obtained an expression to measure changes in the organism's entropy.

We hope this work contributes to a discussion of the relevance of the Second Law of thermodynamics for DEB theory that could lead to a framework to measure exergy (productive energy) flows and exergy degradation efficiencies in organisms [4].

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