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Thermochimica Acta 251 (1995) 363–369

thermochimica
acta

Stability and reliability of ontogenesis ☆

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Received 21 June 1994; accepted 30 August 1994

Abstract

Thermodynamic considerations and experimental data are provided which substantiate energy criteria of reliability and stability of development. The minimum total oxygen consumption over some period of ontogenesis corresponds to the most favourable temperature conditions of development of poikilotermic animals. Another method of determining the stability and reliability of ontogenesis is developed using the notion of the bound dissipation function, which can be determined by study of the discrepancies between direct and indirect calorimetry data.

Keywords: Homeorhesis; Ontogenesis; Reliability; Stability; Thermodynamics

1. Introduction

The problems of stability and reliability in ontogenesis are important not only in theoretical developmental biology but also in many aspects of the artifical rearing and breeding of animals and plants. Special state and processes stability criteria have been worked out using thermodynamics. All these criteria are closely related to extremal principles of thermodynamics which, in the final analysis, are based on the second law. For this reason a thermodynamic approach was taken to considering problems of stability and reliability in developmental processes [1–3].

☆ Presented at the Ninth Conference of the International Society for Biological Calorimetry, Berlin-Schmerwitz, 27–31 May 1994.

SSDI 0040-6031(94)02106-6

2. Thermodynamic basis

Thermodynamic stability and reliability criteria of development are closely related to the principle of minimum energy dissipation [2]: *in a stable state of any thermodynamic system the rate of energy dissipation in it is at a minimum*, i.e.

$$\bar{\psi}_\mathrm{d} = \mathrm{min}. \tag{1}$$

where $\bar{\psi}_\mathrm{d}$ is mean value of the external dissipation function, which is given by

$$\bar{\psi}_\mathrm{d} = \dot{q} \approx \dot{q}_{\mathrm{O}_2} \tag{2}$$

where $\dot{q}$ is the heat production intensity, and $\dot{q}_{\mathrm{O}_2}$ is the oxygen consumption intensity.

Animal development is realized through a constant series of steady states to which the integral principle of minimum energy dissipation can be applied [1–3]: *a non-equilibrium process is stable when the total energy dissipation in the thermodynamic system over the period of time studied is minimal*, i.e.

$$\int_{t_1}^{t_2} \bar{\psi}_\mathrm{d}\,\mathrm{d}t = \int_{t_1}^{t_2} \dot{q}\,\mathrm{d}t \approx \int_{t_1}^{t_2} \dot{q}_{\mathrm{O}_2}\,\mathrm{d}t = \mathrm{min}. \tag{3}$$

3. Criteria of homeorhesis reliability

The integral principle of minimum energy dissipation (Eq. (3)) can assist in studying the action of different external factors on organism development. It is obvious that the total heat production or total oxygen consumption must be minimal at optimal conditions of development. The total oxygen consumption over the period of the first cleavage division in the eggs of the fish *Misgurnus fossilis* in the temperature range 8–28°C is shown in Fig. 1. The temperature range 15–20°C is optimal for the development of *Misgurnus fossilis* embryos, and it can be seen from Fig. 1 that the minimum total oxygen consumption for the first egg cleavage division occurs in this range. The minimum total oxygen consumption also corresponds to the maximum survival of fish embryos during incubation (Fig. 1).

A large amount of data on the effect of temperature on the total oxygen consumption during fish development and insect ontogenesis has been obtained [1–3]. For example, the total oxygen consumption over a pupa period of the flour beetle (*Tenebrio molitor*), the northern house mosquito (*Culex pipiens*), the bee moth (*Galleria mellonella*) and the fruit fly (*Drosophila melanogaster*) is shown in Fig. 2. All these data demonstrated that the relationship between total oxygen consumption and temperature takes the form of parabola. In order to compare different organisms and different stages of development we expressed the temperature dependence of total oxygen consumption in relative values

$$\sum \dot{q}_{\mathrm{O}_2} = a'(\theta)^2 + b'(\theta) + c' \tag{4}$$

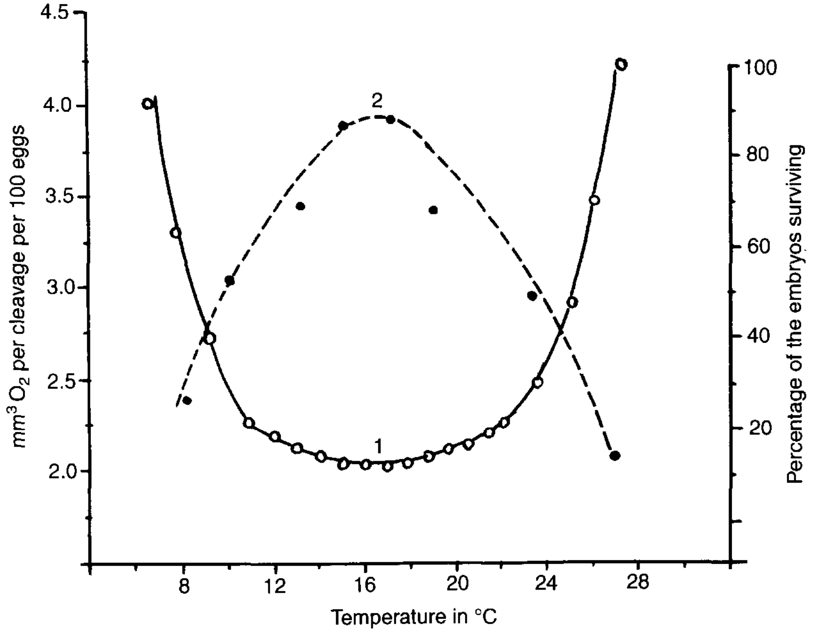

Fig. 1. The total oxygen consumption during one cleavage (1) of loach *Misgurnus fossilis* eggs at different temperatures, and the percentage of surviving embryos (2) at hatching [3].

where $\Sigma\, \dot{q}_{O_2}$ is the total oxygen consumption expressed as a percentage of the total oxygen consumption at the apex of the parabola (taken as 100%). Eq. (4) allows us to introduce two quantitative criteria of ontogenesis reliability [2,3].

The first criterion is a homeorhesis reliability measure

$$M_{hr} = \frac{1}{2a} \qquad (5)$$

where M_{hr} shows in comparable units how one homeorhesis is more reliable than another. The second criterion is an optimal zone of homeorhesis. Evidently there is a certain temperature range within the limits of which the stability of development is nearly the same. We defined this optimal zone as the temperature range within which the total oxygen consumption does not exceed 10% of the oxygen consumption at the apex of parabola [2]. This optimal zone can be determined graphically or by using the formula

$$z_{hr} = \sqrt{\frac{0.4c}{a} + \frac{0.1b^2}{a^2}} \qquad (6)$$

The position (W) of the most stable trajectory of the developmental process (called the *creode* by Waddington [4]) is, from Eq. (4)

$$W = -\frac{b}{2a} \qquad (7)$$

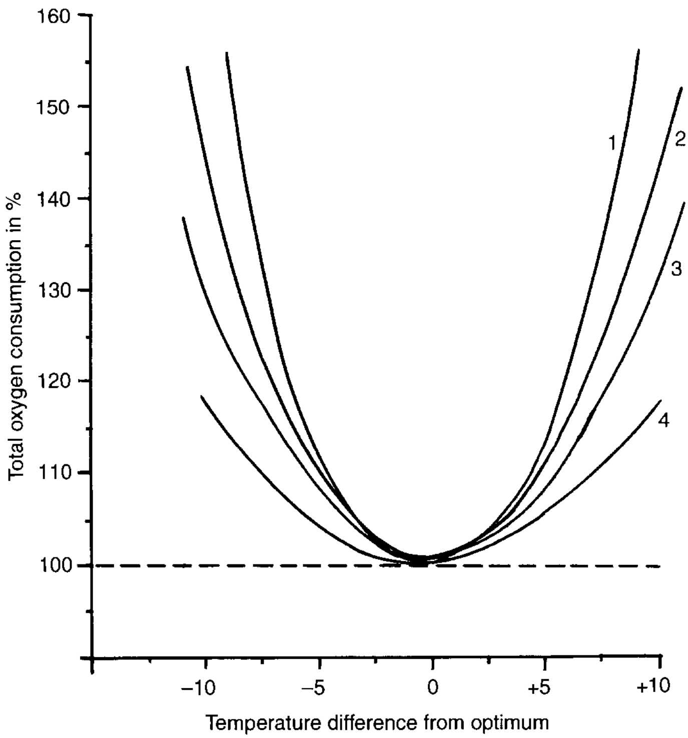

Fig. 2. The total oxygen consumption over the pupae period versus environmental temperature. Total oxygen consumption is presented as the percentage of oxygen consumed at the optimum temperature (taken as 100%) [3]. (1) Flour beetle *Tenebrio molitor*; (2) northern house mosquito *Culex pipiens*; (3) bee moth *Galleria mellonella*; (4) fruit fly *Drosophila melanogaster*.

Values of W calculated using previously reported data on the temperature dependence of total oxygen consumption during development and growth in poikilotermic animals are given in Table 1. It can be seen from the table that the optimal zone becomes wider and the reliability measure increases over the course of animal development, which indicates a perfecting of the reliability of temperature homeorhesis during ontogenesis. The most stable trajectory of development (creode) can be demonstrated using the effect of other environmental factors other than temperature, in particular, the effect of water salinity on marine animals [3].

4. Bound dissipation function

Another method of determining the stability and reliability of ontogenesis can be developed using the concept of the bound dissipation function. The principle of minimum-energy dissipation (Eq. (1)) is based not only on the notion of the dissipation function

Table 1
Reliability measure M_{hr}, optimal zone Z_{hr} and creode W_{T} of temperature homeorhesis for different stages of development in insects and fishes [2]

Species	Stages of development	M_{hr}	Z_{hr}	W_{T}/°C	Ref.
Insects					
Tenebrio molitor	Pupa	0.73	7.2	28.4	7
Galleria melonella	Pupa	1.10	8.2	28.0	8
	Pupa	1.73	11.6	28.0	8
Drosophila melanogaster	Embryo	0.42	6.8	24.5	9
	Larva	1.21	10.3	24.0	9
	Pupa	2.47	14.0	23.6	9
Fish					
Misgurnus fossilis	Cleavage	0.65	7.0	17.1	10
	Cleavage	0.70	7.5	16.8	11
	Gastrulation	0.71	7.5	17.0	11
	Somitogenesis	0.83	8.2	17.2	11
	Heart pulsation	0.53	5.2	17.4	11
Huso huso	Cleavage	0.28	4.8	14.2	12
Salmo irrideus	Cleavage	0.24	4.4	5.3	13
	Gastrulation	0.36	5.5	7.0	13
	Somitogenesis	0.38	5.5	7.4	13
	Heart pulsation	0.56	6.7	8.7	13
	Hatching	0.90	8.5	10.5	13
Oncorhynchus keta	Cleavage	0.25	4.5	8.3	14
	Gastrulation	0.63	7.1	7.3	14
	Heart pulsation	1.39	10.5	7.1	14
	Hatching	1.77	11.9	5.3	14

$$\psi = \frac{T}{V}\frac{\mathrm{d}_i S}{\mathrm{d}t} \tag{8}$$

but also on the external dissipation function (ψ_{d}) and the bound dissipation function (ψ_{u}) from the subdivision [2,3]

$$\psi = \psi_{\mathrm{d}} + \psi_{\mathrm{u}} \tag{9}$$

A proof for this subdivision for a purely chemical system is given below. For such a system, Eq. (8) has the form

$$\psi = \frac{1}{V}\sum_{\rho=1}^{n} A_\rho v_\rho \tag{10}$$

where $v_\rho = \mathrm{d}\xi/\mathrm{d}t$ is the rate of reaction ρ, and A_ρ is the affinity. It is known that

$$A = -\left(\frac{\mathrm{d}G}{\mathrm{d}\xi}\right)_{p,T} = -\left(\frac{\mathrm{d}H}{\mathrm{d}\xi}\right)_{p,T} + T\left(\frac{\mathrm{d}S}{\mathrm{d}\xi}\right)_{p,T}$$

where G is the Gibbs free energy, and H is the enthalpy. Substituting the above in Eq. (10),

$$\psi = -\frac{1}{V}\sum_{\rho=1}^{n}\left(\frac{\mathrm{d}H}{\mathrm{d}\xi_\rho}\right)_{p,T}\cdot v_\rho + \frac{T}{V}\sum_{\rho=1}^{n}\left(\frac{\mathrm{d}S}{\mathrm{d}\xi_\rho}\right)_{p,T}\cdot v_\rho$$

Introducing the symbols

$$\psi_\mathrm{d} = -\frac{1}{V}\sum_{\rho=1}^{n}\left(\frac{\mathrm{d}H}{\mathrm{d}\xi_\rho}\right)_{p,T}\cdot v_\rho = \frac{1}{V}\sum_{\rho=1}^{n} r_{p,T}^{(\rho)}\cdot v_\rho = \dot{q} \qquad (11)$$

and

$$\psi_\mathrm{u} = \frac{T}{V}\sum_{\rho=1}^{n}\left(\frac{\mathrm{d}S}{\mathrm{d}\xi_\rho}\right)_{p,T}\cdot v_\rho \qquad (12)$$

leads to the subdivision given by Eq. (9).

As $\psi_\mathrm{d} = \dot{q}$ and $\psi = \dot{q}_{\mathrm{O}_2}$ [2], ψ_u can be written as

$$\psi_\mathrm{u} = \dot{q}_{\mathrm{O}_2} - \dot{q} \qquad (13)$$

Eq. (13) can be used to check the ψ_u function experimentally.

Table 2 presents data taken from the work by Bell [5] on total oxygen consumption and total heat production during the pupal period of *Galleria melonella* under different temperatures, and the difference between these values expressed as a percentage. It can be seen from these calculations that the total oxygen consumption is minimal and the total bound dissipation function is maximal in the optimum temperature zone. At higher and lower temperatures the discrepancy between the direct- and indirect-calorimetry data decreases. To confirm this, data obtained in the study of hen development [6] are given in Table 3. The data include the calculated oxygen consumption and total heat production for the whole incubation period of hen eggs at different temperatures, and the discrepancy between direct- and indirect-calorimetry data. The data imply that the total ψ function is maximum in the zone of temperature that is optimal for development.

Table 2
Total oxygen consumption $\Sigma\,\dot{q}_{\mathrm{O}_2}$ and total heat production $\Sigma\,\dot{q}$ over the pupal period of the wax moth *Galleria melonella* at different temperatures [5]

θ/°C	Males			Females		
	$\Sigma\,\dot{q}_{\mathrm{O}_2}/(\mathrm{J\,g^{-1}})$	$\Sigma\,\dot{q}/(\mathrm{J\,g^{-1}})$	$\Sigma\,\psi_\mathrm{u}/\%$ [a]	$\Sigma\,\dot{q}_{\mathrm{O}_2}/(\mathrm{J\,g^{-1}})$	$\Sigma\,\dot{q}/(\mathrm{J\,g^{-1}})$	$\Sigma\,\psi_\mathrm{u}/\%$ [a]
25	207	150	27.5	220	167	24.1
30	202	125	38.1	226	150	33.6
35	225	160	28.9	239	160	33.0
40	323	230	29.0	360	253	29.7

[a] Percentage of total oxygen consumption.

Table 3
Total oxygen consumption $\Sigma \dot{q}_{O_2}$, total heat production $\Sigma \dot{q}$ and total bound dissipation function $\Sigma \psi_u$ for the incubation period of hen eggs at different temperatures

	$\theta/^\circ C$					
	35.6	36.7	37.2	37.8	38.9	39.7
$\Sigma \dot{q}_{O_2}/(J\ g^{-1})$	1312	1335	1198	1349	1289	1010
$\Sigma \dot{q}/(J\ g^{-1})$	1134	1134	1009	1059	1061	823
$\Sigma \psi_u/(J\ g^{-1})$	178	201	189	290	228	187
$(\Sigma \dot{q}_{O_2}/\Sigma \psi_u)/\%$	13.6	15.1	15.8	21.5	17.7	18.5

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