Oikos

O18540
Doi, H., Cherif, M., Iwabuchi, T., Katano, I., Stegen, J. C. and Striebel, M. 2010. Integrating elements and energy through the metabolic dependencies of gross growth efficiency and the threshold elemental ratio. – Oikos 119: 752–765.

Appendix 1

(A) Theoretical derivation of the GGE and $\mathrm{TER}_{C:P}$ as a function of body size

(1) NGE for energy as a function of body size
Rem: the symbols used are the same as in Hou et al. (2008) and are thus only briefly defined here. Interested readers are referred to this article if they want to learn more about the meaning of the symbols and the assumptions of the model.

A first step in the process is to express NGE_E (net growth efficiency for energy) as a function of body mass:

$$\mathrm{NGE}_E = \frac{S}{A} \tag{1}$$

where S is the rate of storage of energy in the biomass by a growing organism and A is the rate of energy assimilation from food.
S can be expressed as:

$$S = \gamma B_{\mathrm{syn}} \tag{2}$$

where B_{syn} is the rate of energy used to synthesize new biomass, but not stored into biomass (energetic cost of growth). γ is the ratio of the energy stored in a unit of biomass to the energy expended to synthesize this biomass.

In turn, B_{syn} can be expressed as:

$$B_{\mathrm{syn}} = B_{\mathrm{rest}} - B_{\mathrm{maint}} \tag{3}$$

where B_{maint} is the maintenance metabolic rate and B_{rest} is the resting metabolic rate (includes the energy rates for maintenance, biomass synthesis and digestion).

Both these rates are related to body size and temperature (outside temperature for poikilotherms and internal temperature for homeotherms):

$$B_{\mathrm{rest}} = B_0 m^{3/4} e^{E_r/kT} \tag{4}$$

where B_0 is constant for a given taxon, m is the biomass as an instant t, E_r is the energy activation constant (~0.65 eV), k is Boltzmann constant (8.62×10^{-5} eV/K) and T is temperature in Kelvin.

$$B_{\mathrm{maint}} = B_0 M^{-1/4} e^{E_r/kT} m \tag{5}$$

where $B_0 M^{-1/4} e^{E_r/kT}$ is the mass-specific maintenance metabolic rate and M is the asymptotic or adult body mass for organisms with determinate growth or indeterminate growth respectively.

Equation 2, 4 and 5 combined yield an expression for the relation between S and body mass:

$$S = \gamma B_0 m^{3/4} \left(1 - \left(\frac{m}{M} \right)^{1/4} \right) e^{E_r/kT} \tag{6}$$

On the other hand, A can be rewritten as:

$$A = B_{\mathrm{rest}} + B_{\mathrm{act}} + S \tag{7}$$

where B_{act} is the rate of energy spent on locomotion, feeding and other activities.
B_{act} is assumed to be a multiple of B_{rest}, with a factor:

$$B_{\mathrm{act}} = (f - 1) B_{\mathrm{rest}} \tag{8}$$

where f is the activity scope.
Equation 2, 3, 7 and 8 combined yield:

$$A = (f + \gamma) B_{\mathrm{rest}} - \gamma B_{\mathrm{maint}} \tag{9}$$

The final step to yield the body mass dependence of A is to replace B_{syn} and B_{maint} by their expressions in Eq. 4 and 5:

$$A = B_0 M^{3/4} \left((f + \gamma) \left(\frac{m}{M} \right)^{3/4} - \gamma \frac{m}{M} \right) e^{E_r/kT} \tag{10}$$

NGE_E is the ratio of S to A:

$$\mathrm{NGE}_E = \frac{S}{A} = \frac{\gamma B_0 m^{3/4} \left(1 - \left(\frac{m}{M} \right)^{1/4} \right) e^{E_r/kT}}{B_0 M^{3/4} \left((f + \gamma) \left(\frac{m}{M} \right)^{3/4} - \gamma \frac{m}{M} \right) e^{E_r/kT}} \tag{11}$$

Pulling some factors out of the numerator and denominator and a few simplifications yield the final expression for NGE_E:

$$\mathrm{NGE}_E = 1 - \frac{f}{f + \gamma - \gamma \left(\frac{m}{M} \right)^{1/4}} \tag{12}$$

A few comments on Eq. 12:
Apart from instantaneous and adult body masses, NGE_E depends on only two other physiological parameters that are not consistently related to body size nor temperature, the activity scope f and the ratio of the energy stored to the energy expended in biomass γ.
NGE_E does not depend on temperature. It does depend on the ratio of instantaneous body mass to adult body mass: it reaches its

maximum value $1-\frac{f}{f+\gamma}$ when m/M is almost 0 (i.e. m is negligible in comparison to M); it decreases with an increase in m/M; and is equal to 0 when m is equal to M (i.e. when the organism reaches its adult body mass), thus reflecting the stop in growth that occurs at the adult stage.

(2) GGE for energy as a function of body size

GGE is the NGE multiplied by assimilation efficiency (AE). Hence:

$$GGE_E = AE_E \times NGE_E \qquad (13)$$

There is no clear expectation in the literature on the relationship between AE_E and body size during ontogenetic growth. Experimental data show mixed patterns, with some experiments documenting a significant effect of body size on AE_E (Urabe and Watanabe 1991) and others no effect (Peck et al 2003). In absence of any clear prediction, we assume that there should not be any consistent relationship between AE_E and body size. As a result, GGE_E should show the same size-dependence as NGE_E:

$$GGE_E = AE_E \times \left(1-\frac{f}{f+\gamma-\gamma\left(\frac{m}{M}\right)^{1/4}}\right) \qquad (14)$$

(3) GGE for carbon as a function of body size

GGE_E is the ratio of energy stored in biomass (S_E) to energy ingested (I_E):

$$GGE_E = \frac{S_E}{I_E} \qquad (15)$$

To retrieve GGE_C, one can multiply S_E by C_C:E_C, the ratio of carbon-to-energy in biomass, and I_E by C_F:E_F, the carbon-to-energy ratio in the food ingested:

$$GGE_C = GGE_E \times \frac{C_C}{E_C} \Big/ \frac{C_F}{E_F} \qquad (16)$$

There should be no consistent relationship between carbon-to-energy ratios and body size, resulting in a size-dependence of GGE_C similar to GGE_E. For higher trophic levels, C_C:E_C and C_F:E_F should be close, so that GGE_C and GGE_E should be almost equal.

(4) GGE for nitrogen as a function of body size

GGE_N can be calculated from GGE_E in a similar way to GGE_C, by multiplying it by N_C:E_C, the ratio of nitrogen-to-energy in biomass, and dividing it by N_F:E_F, the nitrogen-to-energy ratio in the food ingested:

$$GGE_N = GGE_E \times \frac{N_C}{E_C} \Big/ \frac{N_F}{E_F} \qquad (17)$$

As for carbon, we assume that there is no significant effect of body size on N_C:E_C and N_F:E_F. Hence, GGE_N should follow the same size-dependency as GGE_E.

(5) GGE for phosphorus as a function of body size

GGE_P can be calculated from GGE_E:

$$GGE_P = GGE_E \times \frac{P_C}{E_C} \Big/ \frac{P_F}{E_F} \qquad (18)$$

where P_C:E_C is the ratio of phosphorus-to-energy in biomass, and P_F:E_P, the phosphorus-to-energy ratio in the food ingested.
P_F:E_P, should not vary with body size in experiments if food is set by experimenters.
P_C:E_C on the other hand is expected to vary with body size. It can be rewritten as:

$$\frac{P_C}{E_C} = \frac{P_C}{m} \Big/ \frac{E_C}{m} \qquad (19)$$

where P_C:m is the percentage of phosphorus in dry weight and E_C:m is the energy content of biomass. E_C:m is independent of biomass, but not P_C:m (Gillooly et al. 2005). Allen et al. derive a mathematical expression for the relation between P_C:m and body mass:

$$\frac{P_C}{m} = \left[P_0\right] + \frac{\alpha M_{ribo} f_P^{RNA}}{4 f_{ribo}^{RNA} \nu_0^{ribo} E_{ATP}} b_0 M^{-1/4} \qquad (20)$$

where $[P_0]$ is the percentage of non-RNA phosphorus in biomass, α is the fraction of metabolic energy allocated to protein synthesis, M_{ribo} is ribosome mass, f_P^{RNA} is the RNA fraction in P, f_{ribo}^{RNA} is the fraction of RNA in ribosomes, is ν_0^{ribo} the ribosome flux (number of peptide bonds per ribosome per second), E_{ATP} is the energy content of ATP and b_0 is the scaling constant for the metabolic rate (see Allen and Gillooly 2009 for a complete definition of the symbols used). According to Allen and Gillooly (2009), these physiological are all independent of size. Hence, the phosphorus content P_C:m should vary with body mass with an approximately –1/4 exponential function.
Combining Eq. 11, 18, 19 and 20 yields the final equation for GGE_P:

$$GGE_P = \left(1-\frac{f}{f+\gamma-\gamma\left(\frac{m}{M}\right)^{1/4}}\right) \times \left(\left[P_0\right] + \frac{\alpha M_{ribo} f_P^{RNA}}{4 f_{ribo}^{RNA} \nu_0^{ribo} E_{ATP}} b_0 M^{-1/4}\right) \Big/ \left(\frac{P_F}{E_F} \times \frac{E_C}{m}\right) \qquad (21)$$

In comparison to GGE_E, there is now an additional negative dependence of GGE_P on adult body mass.

(6) $TER_{C:P}$ as a function of body size

$TER_{C:P}$ can be written as:

$$TER_{C:P} = \left(\frac{GGE_P}{GGE_C}\right) \times \frac{C}{P} = \left(\frac{GGE_P}{GGE_C}\right) \times \frac{C/m}{P/m} \qquad (22)$$

Since GGE_P is proportional to P/m × GGE_C (Eq. 18, 19 and 21), the size-dependence of these three factors should cancel out. Since C/m is not consistently related to body size, then $TER_{C:P}$ should not be affected by body size.

(B) Empirical relationship between relative mass (ratio of measured weight to asymptotic weight) and asymptotic weight in our dataset

The previous section shows that the various elemental GGE vary as a function of m/M, the ratio of measured weight to asymptotic weight. In our study, we are interested in the relationship between asymptotic body size, M, and the various elemental GGE. If there is a correlation between m/M and M in our dataset, whatever the underlying cause is, then we can predict a significant correlation between M and the various elemental GGEs, simply based on this correlation between M and the causal variable m/M.

In our dataset, the relationship between m/M and M is significant for invertebrates and for multicellular organisms (Fig. 1). The correlation is negative. Since m/M effect on the GGE is negative, we thus expect a positive correlation between M and GGE_C and GGE_N respectively. In the case of GGE_P, given the additional direct negative effect of M (Eq. 21), it is difficult to conclude on the overall effect of M without a precise estimate of the correlation between m/M and M on one hand, and of the parameters involved in Eq. 21 on the other hand. It is however safe to conclude that if the correlation is positive, it would be with a shallower slope than for GGE_C and GGE_N.

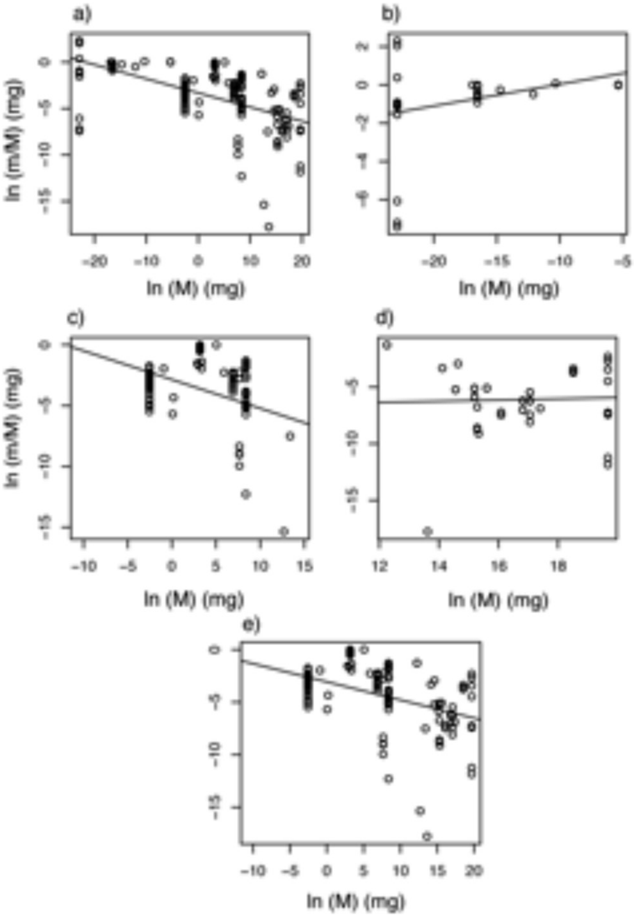

Figure 1. ln–ln relationship between the ratio of measured-to-asymptotic body weight (m/M) and asymptotic body weight (M), a) for all organisms; b) for unicellular organisms only; c) for invertebrates only; d) for vertebrates only; and e) for multicellular organisms (invertebrates + vertebrates). The lines are the linear regressions. The slope is significantly different from 0 for invertebrates ($p=1.04\ 10^{-5}$) and multicellulars ($p<2\ 10^{-16}$).