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Effects of size and temperature on developmental time

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Experiment 4

Soil feedback and relative abundance of plants in the field (Fig. 3) was measured. The abundance of each plant species was measured at 100 different locations within the LTMRS. Locations were randomly chosen, and the presence of all plant species within a 1-m^2 quadrat was recorded at each location. Relative abundance for each species was calculated as the percentage of locations containing that species. This was performed in the summers of 1998 and 2000, and results were pooled. Seeds were collected from each of 61 plant species, and feedback response was determined using similar methods as described above in experiment 1. Regression analysis was used to determine the relationship between plant abundance and soil feedback.

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Competing interests statement

The author declares that he has no competing financial interests.

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Effects of size and temperature on developmental time

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Body size and temperature are the two most important variables affecting nearly all biological rates and times[1–7]. The relationship of size and temperature to development is of particular interest, because during ontogeny size changes and temperature often varies[8–12]. Here we derive a general model, based on first principles of allometry and biochemical kinetics, that predicts the time of ontogenetic development as a function of body mass and temperature. The model fits embryonic development times spanning a wide range of egg sizes and incubation temperatures for birds and aquatic ectotherms (fish, amphibians, aquatic insects and zooplankton). The model also describes nearly 75% of the variation in post-embryonic development among a diverse sample of zooplankton. The remaining variation is partially explained by stoichiometry, specifically the whole-body carbon to phosphorus ratio. Development in other animals at other life stages is also described by this model. These results suggest a general definition of biological time that is approximately invariant and common to all organisms.

The effects of body size and temperature on biological rates and times, including development time, have traditionally been studied separately. There is a rich literature on biological allometry that spans nearly a century[1–3]. The relationships of various attributes of organisms such as metabolic rate, development time and lifespan, to body mass, m, are well approximated by power laws. In endothermic birds and mammals, where body temperature is nearly constant, biological rates and times (t) vary with body size as $t \propto m^{1/4}$ (refs 4 and 5). An equally rich literature on physiology relates many

Box 1
Relationship of equation (3) to Q_{10}

As most biological processes occur in the temperature range T_c = 0–40 °C, the term $(1 + (T_c/T_0))$ in equation (3) differs from unity by at most $40/273 \approx 0.15$. So equation (3) can be well approximated by:

$$a(T_c) = a(T_0)e^{(\bar{E}/kT_0^2)(T_c)}$$

Thus, mass-corrected development time ($t/m^{1/4}$, equation (5)) is inversely proportional to $\exp[(\bar{E}/kT_0^2)(T_c)]$ which becomes a Q_{10} when T_c = 10 °C. We then note that, because T_0 and k are fixed, Q_{10} depends only on $\bar{E}$, the activation energy. Taking an average value of $\bar{E}$ = 0.6 eV gives $Q_{10} \approx e^{0.9} \approx 2.5$. This can also be expressed in terms of the slope of the fitted lines of Fig. 1a–d, which range from $\alpha = -(0.11–0.14)$ per °C. Thus, Q_{10} can be approximated by $\exp(-10\alpha)$. Perhaps of greater importance is to recognize that the conventional Q_{10} factor is only an approximation. The exact expression includes further temperature dependence beyond the purely exponential dependence on T_c. Indeed, if Fig. 1a–d were replotted without the factor $(1 + T_c/T_0)$ in the exponent, the slopes would be 10–15% shallower, leading to a 10–15% error when using Q_{10} to obtain values of a.

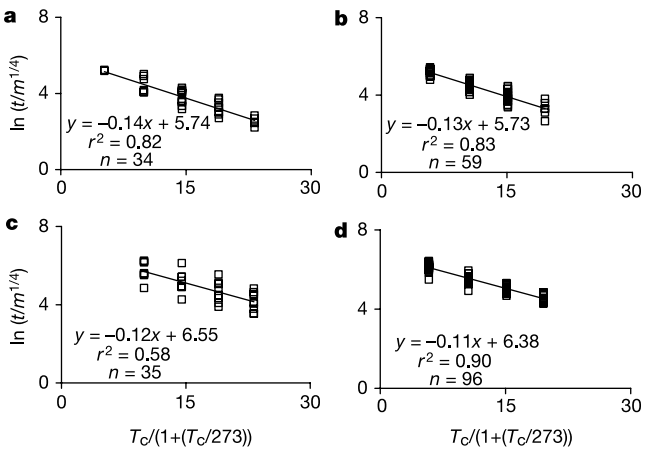

Figure 1 The effect of incubation temperature on mass-corrected embryonic development time for amphibians (**a**), fish (**b**), multivoltine aquatic insects (**c**) and zooplankton (**d**) incubated at different constant temperature. Incubation temperature is given as $T_c/[1 + (T_c/273)]$, in °C over the range 5–25 °C (see Methods); mass-corrected embryonic development time is given as $t/m^{1/4}$, in d per (mass at hatch in g)$^{1/4}$. Lines were fitted using least-squares linear regression. Data obtained from refs 8 and 9.

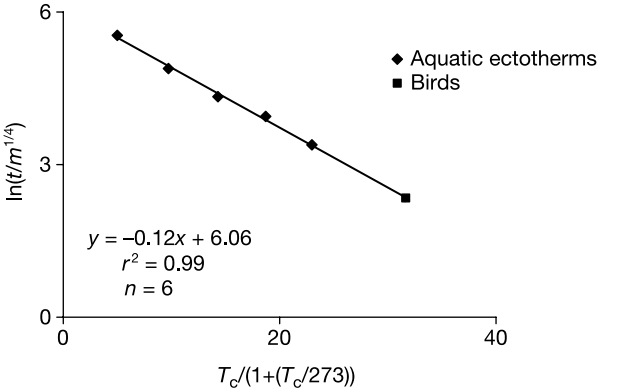

Figure 3 Plot as Fig. 1 but for aquatic ectotherms (data from Fig. 1a–d) and birds. The line is fit using least-squares linear regression to the mean values for all aquatic ectotherms (fish, amphibians, zooplankton, and aquatic insects; diamonds) and the mean value for birds (square) at different incubation temperatures ranging from 5 to 36 °C. Ectotherm data were obtained from refs 8 and 9, bird data from ref. 11.

biological rates and times to temperature[6,7]. Such temperature dependence is traditionally described in terms of Q_{10}, the assumed exponential change in rate for a temperature change of 10 °C. Recently, an allometric model for the effect of body size on growth was formulated based on the allocation of metabolic energy at the cellular level[13,14]. The general equation is:

$$\frac{dm}{dt} = am^{3/4}[1 - (m/M)^{1/4}] \quad (1)$$

where the mass of the organism (m) as a function of time (t) is expressed in terms of the asymptotic mass (M) and a. The parameter a is related to fundamental cellular properties by $a = B_0 m_c/E_c$, where m_c is the mass of an average cell, E_c is the average amount of energy needed to create the cell, and B_0 is the normalization factor for metabolic rate[13], B, which scales with mass as $B = B_0 m^{3/4}$. B_0 is proportional to the biochemical reaction rates for cellular metabolism, and therefore varies with temperature via a standard Boltzmann's factor $\exp(-\bar{E}/kT)$, where T is the absolute temperature (in K), $\bar{E}$ is the average energy for the reaction and k is Boltzmann's constant. As $a \propto B_0$, it has the same temperature dependence, namely $a(T) \propto \exp(-\bar{E}/kT)$. This can also be expressed in the conventional Q_{10} form (Box 1)[15]. The value of $a(T)$ at some temperature T is thereby related to its value at some other arbitrary temperature, T_0, by $a(T)/a(T_0) = [\exp(-\bar{E}/kT)]/[\exp(-\bar{E}/kT_0)]$. Therefore,

$$a(T) = a(T_0)e^{-(\bar{E}/k)((1/T)-(1/T_0))} = a(T_0)e^{(\bar{E}/kT_0)((T-T_0)/T)} \quad (2)$$

Equation (2) can be expressed in terms of °C ($T_c = T - 273$) by setting $T_0 = 273$ K, the temperature at which water freezes and biological reactions cease. This yields the following:

$$a(T_c) = a(T_0)e^{(\bar{E}/kT_0^2)(T_c/(1+T_c/T_0))} \quad (3)$$

Throughout development, the mass of the embryo, m, is small compared to adult mass, M, so equation (1) is well approximated by $dm/dt = am^{3/4}$. When integrated from $m = 0$ at $t = 0$ at a fixed temperature this gives:

$$m = \left(\frac{a(T)t}{4}\right)^4 \quad \text{or} \quad \frac{t}{m^{1/4}} = \frac{4}{a(T)} \quad (4)$$

Substituting equation (3) into equation (4) gives:

$$\frac{t}{m^{1/4}} = \frac{4}{[a(T_0)e^{(\bar{E}/kT_0^2)(T_c/(1+T_c/T_0))}]} \quad (5)$$

which provides a general expression relating development time (t) to body mass (m) and temperature (T_c (in °C)). If body temperature T_c changes during growth, equation (1) must be integrated to reflect the time dependence of the parameter a.

Taking the logarithm of both sides of equation (5) predicts that plots of $\ln(t/m^{1/4})$ versus $T_c/(1 + (T_c/273))$ will yield an approxi-

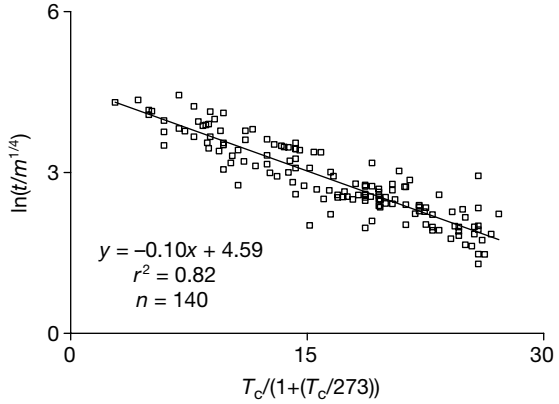

Figure 2 Plot as Fig. 1 but for marine fishes in the field (see Methods). Incubation temperatures ranged from 3 to 30 °C. The line is fit using least-squares linear regression. Data obtained from ref. 10.

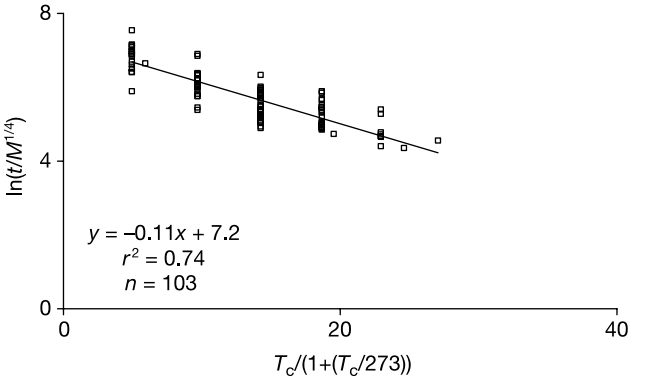

Figure 4 Plot as Fig. 1 but for post-embryonic (hatching to adult) development time for zooplankton (rotifers, copepods and cladocerans) incubated at different constant temperatures ranging from 5 to 30 °C. The line is fit using least-squares linear regression. Data sources listed in Methods.

mately universal straight line with slope, $\alpha = -\bar{E}/kT_0^2$, and intercept, $y_{int} = \ln[4/a(T_0)]$. As $\bar{E}$ and $a(T_0) = B_0 m_c/E_c$ depend on fundamental cellular properties, they, as well as the normalization factor B_0, do not vary significantly across taxa[15]. Therefore, the slope (α) and intercept (y_{int}) should be approximately invariant quantities. We test this prediction using data from the simplest natural 'system' for growth: development time (zygote to hatchling) of eggs. Development of eggs is particularly well suited for assessing equation (5) because the embryo grows in mass as it incorporates the food stores in the egg. Furthermore, development occurs over a wide range of temperatures, from about 5 to 40 °C.

Using laboratory data on embryonic development time from four different groups of aquatic ectotherms (fish, amphibians, aquatic insects and zooplankton), plots of $\ln(t/m^{1/4})$ versus $T_c/(1 + (T_c/273))$ are indeed well fitted by straight lines with similar slopes and intercepts (Fig. 1a–d; see Methods)[8,9]. Similar plots also fit field data on development time for marine fish eggs with a slope and intercept similar to the laboratory studies (Fig. 2) (see Methods)[10]. Furthermore, birds' eggs, which are incubated at much higher temperatures, are also fitted by such plots; pooled data for birds (13 orders, 172 species)[11], using a mean incubation temperature of 36 °C (ref. 8), fall on the same line as the pooled data for aquatic ectotherms (Fig. 3).

The success of the model in describing how size and temperature affect embryonic development time led us to consider whether it might also apply to development at different life stages. As shown in Box 2, the model makes similar predictions for post-embryonic development time (hatch to maturity). Nearly 75% of the variation in post-embryonic development times in zooplankton can be explained by the model. This suggests that equation (5) applies to both embryonic and post-embryonic growth (Fig. 4) (see Methods)[12].

The regression lines for the mass-corrected relationships of development time to temperature (Figs 1–4) also provide an independent means of estimating the parameter a. The temperature dependence of a may be expressed in terms of the slope and intercept using equation (3): $a(T_c) = 4\exp[-(\alpha T_c/(1 + T_c/T_0) + y_{int})]$. Taking average values of $\alpha = -0.12$ per °C and $y_{int} = 6\ln(\mathrm{d\,g^{-1/4}})$ from Fig. 3, this equation predicts $a = 0.65\,\mathrm{g^{1/4}\,d^{-1}}$ for post-embryonic growth of birds at 40 °C, and $a = 0.018\,\mathrm{g^{1/4}\,d^{-1}}$ for post-embryonic growth of cod at 5 °C (ref. 16). These values compare favourably with independent estimates of a derived from fitting empirically measured growth curves[14]. These estimates give nearly the same value of $a = 0.017\,\mathrm{g^{1/4}\,d^{-1}}$ for the cod, and three values that bracket 0.65 for birds (0.47, 1.56, $1.90\,\mathrm{g^{1/4}\,d^{-1}}$)[14]. The fact that these two independent methods give similar values is further evidence that the model captures the effects of body size and temperature on growth.

Moreover, the activation energy for metabolic reactions can be used to predict the slope of the relationships in Figs 1–4. Using the equation $\alpha = -\bar{E}/kT_0^2$ (that is, equation (5)), and an average activation energy for metabolic reactions of 0.6 eV (range between approximately 0.2 and 1.2 eV)[15,17–19], we predict $\alpha = -0.09$ per °C. The closeness of this value to the observed average value of $\alpha = -0.12$ per °C provides support for this model (that is, equation (5)).

We have therefore shown that body size and temperature account for much, but by no means all, of the variation in biological rates and times. Our model, based on first principles of allometry and kinetics, can help to isolate the causes of this still unexplained variation. For example, during post-embryonic growth, unlike embryonic growth, individuals must forage to obtain resources from environments where the availability of nutrients varies. In particular, it is suggested that organisms with higher mass-specific post-embryonic growth rates ($(1/m)(\mathrm{d}m/\mathrm{d}t)$) acquire more phosphorus (P) relative to other elements such as carbon (C) to produce the phosphorus-rich nucleic acids required for more frequent cell divisions and faster growth (that is, the 'stoichiometric growth hypothesis')[20–22]. Thus, faster-growing organisms would be predicted to have lower C:P ratios. In Box 3, we relate this stoichiometric growth hypothesis to our size/temperature model. Figure 5 shows that C:P ratios explain much of the residual variation in Fig. 4.

Many biological times, including cardiac cycle, blood circulation time, and development time (that is, t), increase as the 1/4 power of

Box 2
Extension to post-embryonic growth

The general solution to equation (1) valid for all times is given by

$$\left(\frac{m}{M}\right)^{1/4} = 1 - \left[1 - \left(\frac{m_0}{M}\right)^{1/4}\right] e^{-at/4M^{1/4}}$$

where m_0 is the initial larval mass ($m = m_0$ at $t = 0$). Most zooplankton have determinate growth, and the onset of adulthood is assumed to be at $m = \delta M$; at this size growth ceases and the available energy is diverted to reproduction. We assume $\delta \approx 0.50$–0.90, and is similar across species (see below). The time taken, t_m, to reach $m = \delta M$ is given by

$$\frac{t_m}{m^{1/4}} = \left(\frac{4}{a}\right)\left(\frac{1}{\delta^{1/4}}\right)\ln\left[\frac{(1 - (m_0/M)^{1/4})}{(1 - \delta^{1/4})}\right]$$

Apart from the $\delta^{1/4}$ term and the slowly varying logarithmic factor, this equation for post-embryonic growth (that is, hatch to maturity), is identical in structure to equation (5), which describes embryonic growth. Proceeding as before and using equation (3) for the temperature dependence of a implies that plots of $\ln(t_m/m^{1/4})$ versus $T_c/(1 + (T_c/T_0))$ will yield straight lines whose slopes are the same as those derived from equation (5) for embryonic growth: both should have slopes given by $\alpha = -\bar{E}/kT_0^2$. Their intercepts, on the other hand, should be slightly different: for post-embryonic growth the intercept is given by $\ln[4/a(T_0)] + \ln\ln[(1 - (m_0/M)^{1/4})/(1 - \delta^{1/4})] - 1/4\ln\delta$ rather than simply $\ln[4/a(T_0)]$. The difference between these is rather small; if $m_0/M \ll 1$, δ in the range of 0.50–0.90 yields a correction in the range of approximately 0.50–1.3, a 10–22% increase in the intercept above the value of approximately 6 shown in Fig. 1. The correction depends very little on δ, so δ need not be strictly constant across species. Data for post-embryonic growth for a variety of zooplankton (rotifers, copepods and cladocerans) are plotted in this way in Fig. 4. As can be seen, a straight line is obtained with a slope of −0.11 per °C and an intercept of $7.2\ln(\mathrm{g^{1/4}d^{-1}})$. Because the latter is 17% greater than 6, there is excellent agreement with corresponding values derived from embryonic growth data in Figs 1–3.

Box 3
The relationship to biological stoichiometry

To incorporate the "stoichiometric growth hypothesis"[20–22] we propose that $a(T)$ also depends on the C:P ratio so that $a(T) \propto \exp(-\bar{E}/kT)\lambda(\mathrm{C:P})$, where λ(C:P) is a decreasing function of the C:P ratio. This can be used in equation (5) to predict that growth rates decrease with C:P across species (see Methods). To assess if C:P ratios do in fact decrease with growth rates across species, we plot C:P ratios against the corresponding residuals for zooplankton in Fig. 4 (Fig. 5). Species in Fig. 5 represent all major groups of zooplankton shown in Fig. 4 (cladocerans, calanoid and cyclopoid copepods), except rotifers for which stoichiometric data were not available. We predict an inverse relationship such that species that lie above the fitted line (that is, lower average growth rates) would have high C:P ratios, and vice versa. And, the plot does indeed show that considerable variation about the line in Fig. 4 is explained by differences in the C:P ratios among species. This supports our prediction and suggests that the relationship between size, temperature and biological stoichiometry proposed above may be correct.

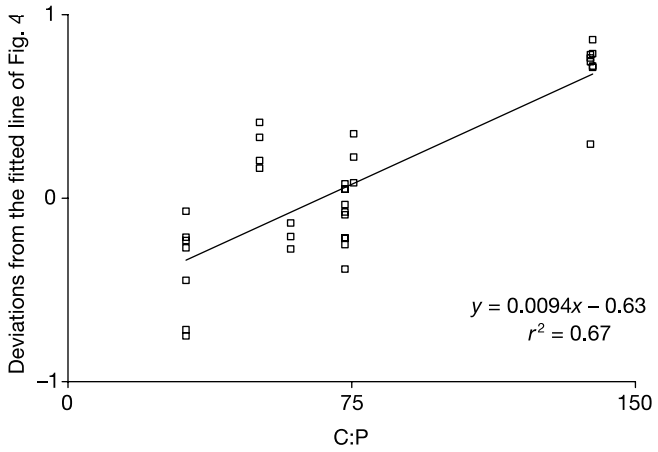

Figure 5 The relationship between deviations for the fitted line in Fig. 4 (that is, $T_c/(1 + (T_c/273))$ versus $t/m^{1/4}$) and whole-body carbon to phosphorus ratios (C:P) for adults of these species. Data sources listed in Methods.

body mass[2,3]. Because all of these times are ultimately related to biochemical reaction rates, they are expected to decrease with temperature via the same Boltzmann factor, $\exp(-\bar{E}/kT)$. Combined, the effects of mass and temperature therefore yield a general definition of biological time:

$$t_B = t(m/m_0)^{-1/4} e^{(-\bar{E}/k(1/T-1/T_0))}$$

$$= t(m/m_0)^{-1/4} e^{-\alpha T_c/(1+T_c/T_0)} \quad (6)$$

where m_0 normalizes mass to some arbitrary value (for example, 1 g) and T_0 normalizes temperature to some arbitrary value (for example, 20 °C). This is the biological time clock. □

Methods

Embryonic development time

Embryonic development times of aquatic ectotherms were collected from compilations of laboratory studies where eggs were incubated at different constant temperatures ranging from 5 to 25 °C (refs 8 and 9). These include mostly freshwater, but some marine, species of both vertebrates and invertebrates (zooplankton: 2 phyla, 7 orders, 29 species; fishes: 7 orders, 21 species; amphibians: 2 orders, 10 species; multivoltine aquatic insects: 3 orders, 10 species). For each species, we included only data from the 'biologically relevant' temperature range required for normal development. Egg sizes were obtained from reference texts and used as an approximation for the mass of species at hatching, m, as the mass at hatch is not often measured. This introduces a maximum possible error of <5% so long as $m \geq 0.8$ times the egg mass. Methods are detailed in refs 8 and 9.

Field data on embryonic development times of marine fish are comparable to the laboratory data, except that T_c was taken as the "prevailing temperature at incubation"[10]. Egg masses were calculated from egg diameters assuming a density of 1 g ml^{-1} (ref. 8).

Post-embryonic development time and biological stoichiometry

Most post-embryonic development times and adult body masses were obtained from a compilation of published data[12], though some additional data were acquired for genera under-represented in this compilation. These include cladocerans (*Daphnia*[23,24], *Diaphanosoma*[24], *Ceriodaphnia*[25], *Bosmina*[26]), and species of cyclopoid[27,28] and calanoid copepods[29]. Adult body masses for these species were estimated in the same manner as in the compilation. For Box 3, whole-body C:P ratios were obtained for as many of the species shown in Fig. 4 as possible. The stoichiometric ratios were published values for adults of those species, or adults of species from the same genus and similar body size[21,30].

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