Universal and morphological exponents for metabolic biological growth

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Abstract. In this work we investigated the biological growth exponents and we showed that they obey a combination of universal and empirical morphological exponents. We applied these results for fishes and we obtained the exponents that describe their metabolic growth, and in addition we showed the influence of the exponents on the growth and the maturation time. We discuss the need to review some of the old empirical growth equations to give a better account of the data.
Keywords Universal exponent, Morphological exponent, Metabolic growth

1. Introduction

The large diversity of forms and size of the living beings would at first glance induce us to believe that no quantitative universal law could describe their behavior. On the other hand, since Darwin's evolution theory, we know that all living beings have a common origin and consequently we could expect common features underlying the basic mechanism. Based on that view, one could ask a question such as is there a universal law for growth? The last decades have seen a large number of empirical evidence and theoretical works that point towards two major simple rules: First, a strict relationship between biological growth and metabolic rates. Second, the existence of universal laws for metabolic rates, and consequently for the growth phenomena. Moreover, beyond the most optimistic expectation those laws are simple and universal.

The dependence of biological growth on the metabolic rates have been universally accepted. As such, it is common sense that the basal metabolic rate B obeys an allotropic rate of the form [1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11]

$$B = b_0 M^\alpha, \tag{1}$$

where M is the mass of an average individual of a given species, b_0 is a constant and α is an exponent. However, more than a century was not enough to fix the metabolic exponent α.

In this work we call attention to the existence of universal and specific exponents in biological growth. In particular, we investigated the Bertalanffy equation [1, 2]

$$L(t) = L_\infty \left[1 - e^{-(t+t_0)/\tau_\alpha} \right], \tag{2}$$

where $L(t)$ is the length as function of time, τ_α is a growth time we shall discuss later, and t_0 is obtained by the animal size at birth. This equation has been used for decades and it is still used nowadays in order to fit the growth of fishes. We shall present here a generalization of this equation. Nevertheless this relationship has been used in many situations, and we shall show here that if we need a more precise fit of the available data we have to rewrite this equation into a more general form, see Eq. (9).

2. Growth exponents

In this section we come to the central point of this work, the relationship between the exponents. Our starting point is that the growth mechanism is determined by the metabolic rate in such a way that the gain of mass at each time interval is due to major contributions: one which is proportional to the metabolic rate, which is the necessary energy to mass increment; the second term is the loss of matter that is proportional to the mass itself. Then it is given by

$$\frac{dM}{dt} = c_1 M^\alpha - c_2 M \,, \tag{3}$$

where the second term on the right hand side is a decay term which is proportional to the mass. This equation yields

$$M(t) = M_\infty \left[1 - (1 - \epsilon_\alpha) e^{-t/\tau_\alpha} \right]^\delta \,, \tag{4}$$

where

$$\epsilon_\alpha = \chi^{\frac{1}{\delta}} \,. \tag{5}$$

Here $\chi = M_0/M_\infty$, with $M_0 = M(0)$ as the initial mass, $M_\infty = M(\infty) = (c_1/c_2)^\delta$ as the saturation mass, and $\delta = (1 - \alpha)^{-1}$ as a universal exponent, because it depends only on α which is a universal parameter. Here

$$\tau_\alpha = \frac{\delta}{c_1} M_\infty^{1/\delta} = \frac{\delta}{c_2} \,, \tag{6}$$

is the average time of growth. Although the expression χ could be extremely small, ϵ_α is not. For example for $\alpha = 3/4$, $\delta = 4$, a small $\chi = 0.01$, gives $\epsilon_{\alpha=3/4} \approx 0.32$, which is a considerable amount compared with 1. Consequently, it can not be neglected in Eq. (4). However, there is a "normal procedure" in the literature that consists of defining a time t_0 as in Eq. (2) as $\exp(-t_0/\tau) = 1 - \epsilon_\alpha$. Even in the particular situation where we consider $\epsilon_\alpha = 0$, we can not consider Eq (2) as a good way to describe the growth phenomena, as we shall see below.

For the value of α we have two extreme views: The classical works of Bertalanffy [1, 2], which associates the metabolic rate to heat dissipation, being in this way proportional to the surface area

$$B \propto V^{2/3} \propto M^{2/3}. \tag{7}$$

From these works it follows that $\alpha = 2/3$. The works of West et al [3, 4, 5] attribute the metabolic rate to the energy necessary to feed each cell through the cardiovascular

network. Their work suggest that the allotropic exponents should be multiples of $1/4$ and that $\alpha = 3/4$.

Recent results show that in macroecology the predator-prey power law biomass scales as well with $\alpha \approx 3/4$, which indicates that very different communities of species exhibit similar high-level structure and function [6, 7]. That conclusion was obtained through a massive amount of data for energy flows within the food chain for both terrestrial and aquatic biomes.

In table 1 we have the values of α given by several authors [9, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21], for more details see White and Seymours [22]. We note that for all the values but the second, we have $2/3 < \alpha < 3/4$. The empirical data gives the average value for $\tilde{\alpha} = 0.72 \pm 0.02$ which if closer to $\alpha = 3/4$ than $\alpha = 2/3$.

The major exponents are connected, which give us important restriction for the growth exponents. First, the relationship between the mass and the length is given by

$$M \propto L^{\lambda}, \tag{8}$$

we shall call here λ the morphological exponent. Note that due the large diversity of forms we do not expect λ to be a universal exponent as α is. However, surprisingly it is remarkably close to 3, see table 2.

Fish growth is an important subject with scientific and practical applications [23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 38, 39]. Now we will suppose that a fish has a length $L(t)$ given by

$$L(t) = L_{\infty} \left[1 - (1 - \epsilon_{\alpha}) e^{-t/\tau_{\alpha}} \right]^{\gamma}. \tag{9}$$

Observe that it generalizes eq. (2). To go beyond an empirical equation, we have to determine γ. Therefore, we consider a lateral elliptical area, with major axis $R_1(t)$, and minor axis $R_2(t)$ given by

$$R_i(t) = R_{i,\infty} \left[1 - (1 - \epsilon_{\alpha}) e^{-t/\tau_{\alpha}} \right]^{\beta_i}, \tag{10}$$

with $i = 1, 2$. It is quite natural to consider the fish as having a uniform and isotropic density, then we have

$$M \propto R_1 R_2 L \propto \left[1 - (1 - \epsilon_{\alpha}) e^{(-t/\tau_{\alpha})} \right]^{\delta}, \tag{11}$$

where

$$\delta = 2\beta + \gamma, \tag{12}$$

where we consider $\beta = (\beta_1 + \beta_2)/2$ the average exponent for lateral growth. Since most of the data refer to $L(t)$, we do not have precise experimental information about the R_i. Consequently there is no reason to keep two β_i. For those with access to more detailed information we would suggest to obtain β_1, β_2 and to check out the difference $\frac{|\beta_1 - \beta_2|}{2\beta}$, which we believe to be a small number. In any case, it does not affect our analysis. Even for the exponents β and γ, we show here that there is not enough data to determine the difference between them.

b_0	2.6	1.8	2.3	4.3	4.2	3.4	3.8	4.1	3.2	4.0	3.7
α	0.74	0.76	0.731	0.69	0.71	0.71	0.71	0.69	0.73	0.686	0.712
Ref	[9]	[12]	[13]	[14]	[15]	[16]	[17]	[18]	[19]	[20]	[21]

Table 1. Basal metabolic rate, $B = b_0 M^\alpha$. All regressions were calculated to standardize units (BMR in ml O_2 h^{-1}, M in g). The averages are $\tilde{\alpha} = 0.72 \pm 0.02$ and $\tilde{b}_0 = 3.4 \pm 0.7$

Fish	Ref	λ	$\tau_{2/3}$
Gymnosarda unicolor	[26]	3.065	2.326
pinirampus pirinampus	[27]	2.945	3.333
pseudopaltystoma fasciatutum	[27]	3.126	7.692
Zungaro jahu	[27]	3.228	7.813
pseudopaltystoma corruscans	[27]	3.172	7.874
dolphinfish Coryphaena hippurus (male)	[28]	3.144	0.977
dolphinfish Coryphaena hippurus (female)	[28]	2.848	0.970
Protosalanx hyalocranius	[29]	2.990	0.341
oedalechlus labeo (male)	[30]	2.975	7.463
oedalechlus labeo (female)	[30]	3.014	5.525
opsarrichthys bidens (male)	[31]	3.150	3.226
opsarrichthys bidens (female)	[31]	3.050	3.846
Sander Lucioperca	[32]	3.010	6.667

Table 2. Parameters λ and the growth time $\tau = \tau_{2/3}$ for each fish. The average λ is $\tilde{\lambda} = 3.06 \pm 0.09$.

α	δ	γ	β
2/3	3	1	1
3/4	4	4/3	4/3
0.72 ± 0.02	3.6 ± 0.1	1.17 ± 0.05	1.20 ± 0.05

Table 3. Values of δ, β and γ from the values of α. In the first two lines we use the expected value $\lambda = 3$, in the last line we use the empirical $\lambda = 3.06 \pm 0.09$.

From the relationship between Eq. (4) and Eq. (8) we get

$$\gamma = \frac{\delta}{\lambda}, \tag{13}$$

and

$$\beta = \frac{\delta}{2\lambda}(\lambda - 1). \tag{14}$$

Now we will analyze the relationship between our equation and the data existing in the literature, and we see that $\gamma = \beta = 1$ only for $\lambda = \delta = 3$ in discordance with the available data.

In Table 2 we show the values of the parameters for several species of fishes. There we display the empirical values of λ and the growth time τ obtained using Eq. (2). Most

of the authors treat the data with a large number of decimals, however, if we consider the standard deviation we see that the alleged accuracy is exaggerated and we have to look at those data with care. The major problem however lies in the many different ways to treat the data.

In table 3 we obtain several exponents from the values of α and Eq. (13) and Eq.(14). For the first and second line we take $\lambda = 3$. For $\alpha = 2/3$, Bertalanffy, we get $\delta = 3$, and both $\gamma = \beta = 1$. For $\alpha = 3/4$ we get $\delta = 4$ and $\gamma = \beta = 4/3$.

From the empirical values $\alpha = 0.72 \pm 0.02$ and $\lambda = 3.06 \pm 0.09$ from table 2, we get $\gamma = 1.17 \pm 0.05$ and $\beta = 1.20 \pm 0.05$. From both second and third line we note that both β and γ are always great than 1, consequently the simple Bertalanffy equation, Eq. (2), does not apply and if we want more precise information we need to use the more complete form Eq. (9). Table 3 shows as well a very small difference between the exponents β and γ. Since $\beta - \gamma \propto \lambda - 3$, and λ is very close to 3, $\bar{\lambda} = 3.06 \pm 0.09$, it is not surprising that we get the average values, $\bar{\beta} \approx \bar{\gamma}$. Indeed, from the available data β and γ are very close, and for this particular issue more precise data are need to definitive conclusion. Thus, we can conclude that $\gamma \approx \beta > 1$, and we need to replace Eq. (2) by Eq. (9).

3. Growth Time

The ratio between the two growth times is given by

$$\frac{\tau_{\alpha 1}}{\tau_{\alpha 2}} = \frac{c_2(\alpha_2)}{c_2(\alpha_1)} \left(\frac{1 - \alpha_2}{1 - \alpha_1} \right) . \tag{15}$$

If we consider c_2 independent of α then, for example $\tau_{3/4}/\tau_{2/3} = 4/3$. However, as we shall see below this naive argument does not apply, indeed both c_1 and c_2 must be strongly dependent on α.

We now examine the relation between two growth times, for two different α, in a more precise way. Since the total time evolution must be independent of α, we define

$$\eta = \frac{1}{\tau M_\infty^2} \int_0^\infty \left[M_{2/3}(t) - M_\alpha(t) \right]^2 dt , \tag{16}$$

which must be minimized to reduce spurious differences. To avoid a cumbersome notation let us take $\tau = \tau_{2/3}$, $\epsilon = \epsilon_{2/3} = \chi^{1/3}$, such that $\epsilon_{3/4} = \epsilon^{3/4} = \chi^{1/4}$.
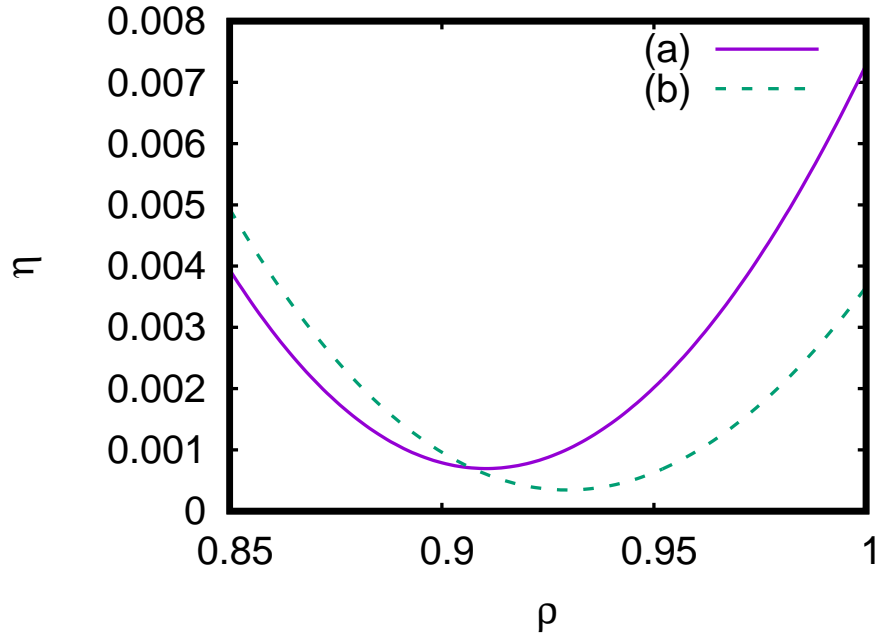
For $\alpha = 3/4$, we obtain

$$\eta = f_1 + f_2 + g , \tag{17}$$
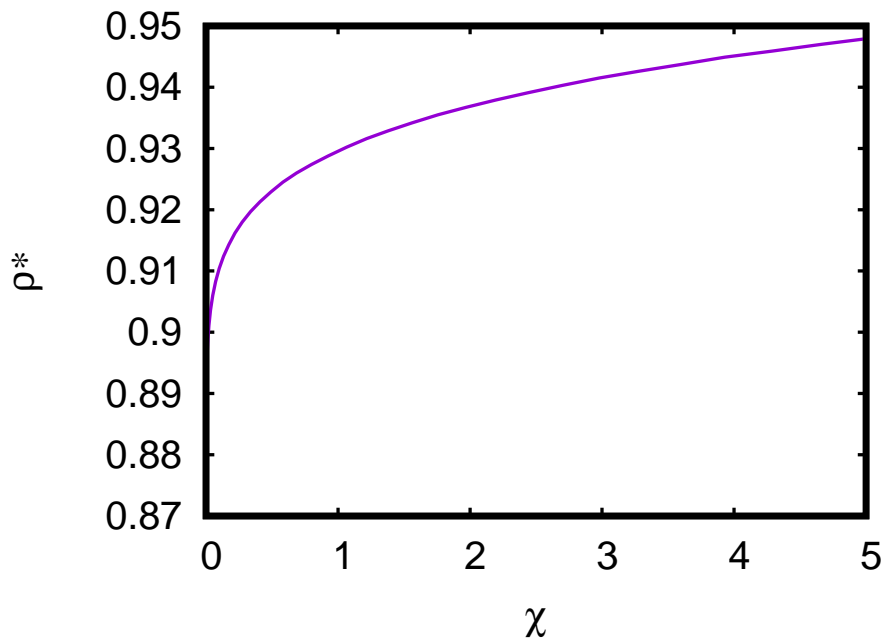
where $\rho = \tau_{3/4}/\tau_{2/3}$ and

$$f_1 = \sum_{i=1}^{3} \sum_{j=1}^{3} \frac{A_i A_j}{i + j} \tag{18}$$

$$f_2 = \rho \sum_{i=1}^{4} \sum_{j=1}^{4} \frac{B_i B_j}{i + j} \tag{19}$$

$$g = -2\rho \sum_{i=1}^{3} \sum_{j=1}^{4} \frac{A_i B_j}{i\rho + j} , \tag{20}$$

Figure 1. η as a function of ρ. Curve (a) We use $\chi = M_0/M_\infty = 10^{-3}$, which gives $\epsilon = 0.1$, we observe a minimum at $\rho* = 0.91$; curve (b) $\chi = 10^{-2}$, we have a minimum at $\rho* = 0.93$.

Figure 2. The ratio between the growth times $\rho*$ as a function of the mass ratio $\chi = M_0/M_\infty$. The χ axis is multiplied by 10^2.

where $A_i = \binom{3}{i}(\epsilon - 1)^i$ and $B_i = \binom{4}{i}(\epsilon^{3/4} - 1)^i$. In this way, η depends on the ρ and ϵ. For a given ϵ, η has a minimum $\frac{\partial \eta}{\partial \rho} = 0$ for $\rho = \rho*$.

In Fig. 1 we plot η as a function of ρ. There we see the ratio $\chi = M_0/M_\infty$ influences the growth time, i.e., the minimum of η. In curve (a), $\chi = M_0/M_\infty = 10^{-3}$, which gives $\epsilon = 0.1$, with the minimum at $\rho* = 0.91$; in curve (b) we have $\chi = 10^{-2}$, which gives $\epsilon = 0.215$, we see that now η has a minimum of $\rho* = 0.93$. Since for fishes $10^{-3} < \chi < 10^{-2}$ is a reasonable range for χ, from that we can conclude that we have decreases in ρ of less than of 10%, and not an increase as suggested by Eq. (15). In this way it becomes clear that the coefficients c_1 and c_2 are strongly dependent on the metabolic law, i.e on α. It is very important to notice as well that a very small χ will demand a bit more of growth time.

In Fig. 2 we plot the value of $\rho*$, which minimizes η as function of χ. Here, we multiply the χ axes by 10^2. The ratio $\rho*$ increases monotonically as χ increases. In this way, we can say that fishes with small χ would have the growth time more affected. However, this fraction is very small, i.e., an order of magnitude in χ will affect only 2%. Altogether, we can say that the growth time will be not affected by the metabolic exponent α, neither by χ. Consequently, the growth time is a very robust concept.

4. Maturation time

We now want to define the time parameter directly associated to reach the maturation mass according to its final mass. This maturation time can be known considering that the maturation mass finds the ideal value in $1 - \exp(-1) \approx 63\%$ of its maximum mass M_∞. From Eq. (4), the maturation time τ^* can be written as

$$\tau^* = \frac{M(t)}{M_\infty} = \tau(\alpha) \ln \left[\frac{1 - \epsilon_\alpha}{1 - (1 - e^{-1})^{1-\alpha}} \right], \tag{21}$$

where we have $\epsilon_\alpha \leq (1 - e^{-1})^{1-\alpha}$.

In Fig. (3) we show τ^* as a function of χ, for different values of α. We take τ^* in units of $\tau(\alpha)$. We can see that both curves decrease with χ, but there are considerable numerical difference between them. We see here a very large difference between the maturation time and the growth time, and how it is affected by the exponent α. This difference is higher than those observed in Figs. (1) and (2). Indeed, this is really something worth to observe in experiments.

5. Conclusion

In conclusion we have investigated the general equations for growth in animals, starting from the basic metabolic rate that states that $B \propto M^\alpha$. From this we determine that lateral growth exponent β and the longitudinal growth exponent γ as function of the the exponent δ and of the morphological exponent λ. The morphological exponents β and γ are such that $1 < \gamma \approx \beta \leq 4/3$. In any case the precision is enough to state that they are
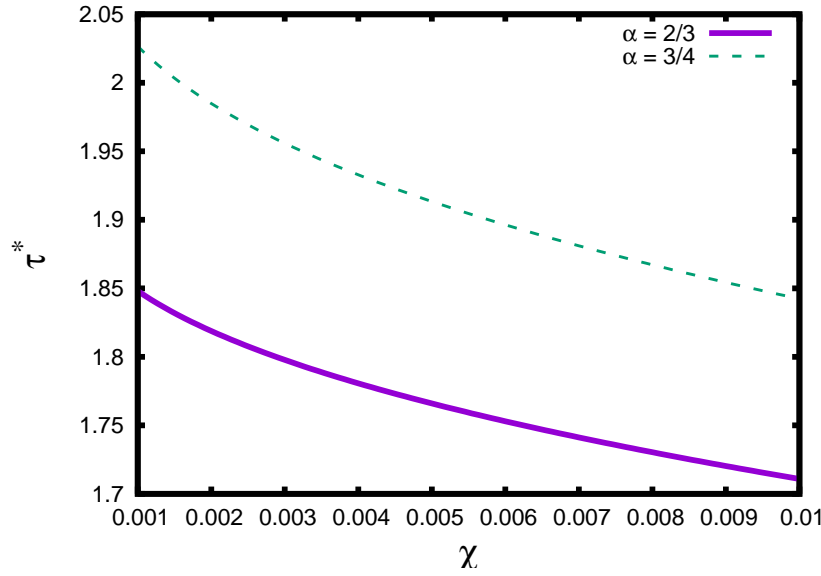
Figure 3. τ^* as a function of χ for $\alpha = 3/4$, upper curve, and $\alpha = 2/3$, lower curve.

different from 1 as exposed in Eq. (2) and consequently the use of Eq. (9) is necessary. We hope that new data could be used to verify the value of the exponents and in addition we expect that researchers with experimental data could run it again using Eq. (9) to validate the exponents. In addition to the exponents the major practical information coming from the analysis are the growth and maturation time, which are important in the laboratory, in fish farming, in fisheries, and for ecological modeling. We conclude that the growth time is very robust independent of the metabolic exponent. However, the maturation time is very sensible to rate $\chi = M(0)/M_\infty$ and α. Unfortunately, the results existing in the literature come from different statistical methods used for treatment of the data, as well most of them do not state the measurement error. Thus it is urgent to make this procedure more uniform.It would also be very important to see if the growth time is affected by stress such as in competition [33, 34, 35, 36, 37]. A more sophisticated theory is necessary to take into account the influence of the temperature in the fish metabolism [38, 39]. However, this goes beyond the objective of this work.

Acknowledgments

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