

A theoretical analysis of the growth process of an organism and its dependence on various allometric relations

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ABSTRACT

A new mathematical model regarding the growth process of an organism is proposed, based on the role of surplus power (*i.e.* power intake minus metabolic cost) and having an allometric dependence on mass. Considering its use in growth, a differential equation has been formed, similar to the von Bertalanffy growth function (VBGF). The time dependence of mass and growth rate, obtained from this equation, has been shown graphically to illustrate the roles played by scaling exponents and other parameters. Concepts of optimum mass, saturation mass and the mass corresponding to the highest growth rate have been discussed under the proposed theoretical framework. Information regarding the dependence of effective growth duration on various parameters has been found graphically. The time of occurrence of the highest growth rate and its dependence on various parameters have been explored graphically. A new parameter (ρ) has been defined, which determines the availability of surplus power at different stages of the growth process of an organism. Depending on its value, there can be three distinctly different modes of growth phenomenon, reflected in the change of surplus power with time. The variations of growth and reproduction efficiencies with time and mass have been shown for different values of the scaling exponent. The limitation regarding the practical measurement of growth rate has been discussed using the present model. Some aspects of length-biomass allometry have been explored theoretically and the results have been depicted graphically.

Keywords: Allometric Scaling in biology; Von Bertalanffy Growth Function; Biological Growth Model; Growth & Reproduction Efficiency; Length-Biomass Allometry; Metabolism

1. INTRODUCTION

On the basis of experimental evidence as well as theoretical formulations it has already been established that the rates of energy intake and energy loss of a living organism have power-law (like $y = ax^b$) dependence on the mass of the organism [1-5]. Therefore, one can represent the rate of energy intake (P_1) and rate of energy loss (P_2) by $C_1 m^{\sigma_1}$ and $C_2 m^{\sigma_2}$ respectively; where C_1 and C_2 are the constants of proportionality, and σ_1 and σ_2 are the corresponding allometric scaling parameters.

The difference between P_1 and P_2 is known as the rate of production of surplus energy ($E_s = P_1 - P_2$) of the organism which is spent mainly for growth and reproduction processes [6-8]. One can express this surplus energy production rate or *surplus power* (E_s) as

$$E_s = C_1 m^{\sigma_1} - C_2 m^{\sigma_2}. \quad (1)$$

Eq.1 can also be derived from the theory of universal phenomenological growth that may be described by a simple law which is expressed as

$$dY(t)/dt = \alpha(t)Y(t). \quad (2)$$

Here, $\alpha(t)$ is a time dependent quantity which represents the specific growth rate of a given variable $Y(t)$. From Eq.2, different types of growth model can be derived. The "Class U1" solution of Eq.2, as described by Castorina *et al.* [9], gives Gompertz law [10] which is largely applied to describe economical and biological growth phenomena like tumor growth pattern etc [11,12]. Castorina *et al.* described Eq.1 as the "Class

U2" solution of **Eq.2** [9].

Over the past few decades, several efforts have been made to determine the value of two scaling parameters σ_1 and σ_2 . In the study of von Bertalanffy, an assumption of $\sigma_2 = 1$ was specified [13,14]. Some studies reveal that the metabolic cost is directly proportional to the mass of an organism, implying $\sigma_2 = 1$ [4,7]. Debates are still going on over the value of σ_1 . People attempted to explain the value of σ_1 with the help of either metabolic theory of ecology or dynamic energy budget theory. The metabolic theory of ecology is based on the idea that the transport of resources takes place through a fractal-like branching network [4,15]. It predicts σ_1 to be $3/4$, supported by different experimental observations. The theory of dynamic energy budgets is based on the concept that the rates of basic physiological processes are proportional to body surface area, implying $\sigma_1 = 2/3$ [16,17]. A. R. P. Rau offered an explanation for the values of scaling parameters, on the basis of Poiseuille's law of fluid flow [18]. The chemiosmotic theory of energy transduction, combined with the method of quantum statistics, is also applied to explain the variation in scaling exponents [19]. Many such investigations show that $\sigma_1 \geq 2/3$. In some cases, it may be equal to $3/4$. Vogel showed that biological processes are controlled by different physical processes like convection, diffusion etc. and the process of mass transport is different for different molecules in an organism [20]. da Silva *et al.* explained the variation of σ_1 with the help of physical processes like diffusion, convection and anomalous diffusion for different organisms [21,22]. According to the study of Economos [23], the geometry of body surface, which is different for different organisms, is related with energy intake of the organism. da Silva *et al.* [22] compared the exponent of basal metabolic rates for different organisms and proposed a theoretical explanation for the different values of that exponent. So, growth process can be studied using different values of these scaling exponents.

It has been found through some research [5-7] that, at the initial stage of growth the surplus power (E_s) increases with mass and then it decreases after reaching its peak value at a mass which is known as the *optimum mass* [7]. Based on this fact, we have shown in our earlier studies that $\sigma_2 > \sigma_1$ [24,25]. Thus, the scaling exponent for metabolic cost is found to be greater than the exponent for energy intake. This is an important conclusion which is also found to be valid according to the studies of West *et al.* [26]. In the present article, we have studied the growth process theoretically, through a model developed by us on the basis of the relation between growth rate and surplus power. Using this mathematical model, an exhaustive analysis of some important aspects

of growth mechanism has been made.

2. MODEL FORMULATION

In the present study, we have taken $\sigma_2 = 1$, under the consideration that metabolic cost is proportional to the body volume (which is directly proportional to mass), in accordance with some studies [3,7,24,27]. Using this value, **Eq.1** is expressed as

$$E_s = C_1 m^{\sigma_1} - C_2 m. \quad (3)$$

The above expression of E_s has been used in all further calculations in the present article. Since excess energy is mainly used for growth and reproduction, these processes would stop if the surplus power (E_s) ever becomes zero in the life of an organism [7,8]. For a certain value of m (say M_h) we have $E_s = 0$, as evident from the functional form of E_s . Using **Eq.3**, we get

$$M_h = (C_1/C_2)^{1/(1-\sigma_1)}. \quad (4)$$

Apart from the processes of growth and reproduction, some excess energy is always required for repair and also to sustain biological processes in situations like sudden environmental fluctuations etc. According to Kozlowski [6] and Sebens [7], some surplus energy (E_s) is always required for a healthy survival of the organism. Therefore, taking $E_s > 0$, **Eqs.3** and **4** yield the following relation

$$m < (C_1/C_2)^{1/(1-\sigma_1)} \equiv M_h. \quad (5)$$

Thus, the growth process must stop before reaching the point where $m = M_h$. In any growth process, as $t \rightarrow \infty$, mass becomes asymptotic to a certain value (say M_a) where $M_a < M_h$. The expression of M_a , the highest attainable mass, has been derived later in this article.

According to some studies [24,25], an organism has a natural tendency to attain the optimum mass (M_{opt}) or energetic optimum size (EOS), which corresponds to the greatest surplus power (E_s) [8,12,21]. For E_s to be maximum at $m = M_{opt}$ we must have

$$1) \frac{dE_s}{dm} = 0 \quad \text{and} \quad 2) \frac{d^2 E_s}{dm^2} < 0 \quad \text{at} \quad m = M_{opt}.$$

The first of the above conditions gives us the following expression of optimum mass (M_{opt})

$$M_{opt} = (C_1 \sigma_1 / C_2)^{1/(1-\sigma_1)}. \quad (6A)$$

Applying the second condition we get

$$\sigma_1 < 1. \quad (6B)$$

Substituting $m = M_{opt}$ in **Eq.3** from **Eq.6A**, the maximum surplus power (E_{sM}) is obtained as

$$E_{sM} = C_1 (C_1 \sigma_1 / C_2)^{\sigma_1/(1-\sigma_1)} - C_2 (C_1 \sigma_1 / C_2)^{1/(1-\sigma_1)}. \quad (7)$$

The difference between the rates of energy intake and energetic cost can be termed *scope for growth* [28] and *energy surplus* [29] depending on which energetic costs are included. If the costs of building gonad are included then this difference is truly *scope for growth*. If only the metabolic maintenance costs are included, this difference is an *energy surplus*, used mainly for growth and reproduction. Experimental observations suggest that the energy allocated for reproduction has an allometric dependence on mass [7,21,30]. Therefore, the rate of energy allocation for reproduction (E_p) can be expressed as

$$E_p = C_3 m^{\sigma_3} \tag{8}$$

where σ_3 is the allometric scaling exponent and C_3 is the proportionality constant for the rate of energy spent for reproduction. Both C_3 and σ_3 are positive quantities. In the present study, we have taken $\sigma_3 = 1$, as proposed by Sebens [7]. Using this value, **Eq.8** is written as

$$E_p = C_3 m \tag{9}$$

The above expression of E_p has been used in all further calculations in this article. The part of the surplus power (E_s) which is not used for reproduction, is mainly used for the growth process. Therefore, the rate of energy allocation for growth (E_g) is given by

$$E_g = E_s - E_p = C_1 m^{\sigma_1} - (C_2 + C_3)m \tag{10}$$

This energy (E_g) causes the mass to increase. Therefore, the rate of variation of mass with time can be expressed as (with proportionality constant scaled to unity)

$$E_g = dm/dt = C_1 m^{\sigma_1} - (C_2 + C_3)m \tag{11}$$

The above equation is similar in form to the von Bertalanffy growth function (VBGF), which is basically a descriptive mechanistic model derived for fish growth rate, based on a simple mass balance equation [13]. But, instead of two constants of proportionality, we have three constants of proportionality to incorporate separately the effects of energy intake, metabolic cost and reproduction cost in the growth process.

The growth process continues as long as E_g remains non-zero. As the organism reaches the state of maximum attainable mass (M_a), E_g becomes zero. Therefore, from **Eq.11**, we obtain

$$M_a = (C_1/C)^{1/(1-\sigma_1)}, [C = C_2 + C_3] \tag{12}$$

with $m = M_0$ at $t = 0$, the solution to **Eq.11** is given by

$$m(t) = \left[C_1/C (1 - e^{-\beta t}) + M_0^{1-\sigma_1} e^{-\beta t} \right]^{1/(1-\sigma_1)} \tag{13}$$

$$[\beta = C(1 - \sigma_1)]$$

Using **Eqs.12** and **13** can be expressed as

$$m(t) = \left[(M_a)^{1-\sigma_1} (1 - e^{-\beta t}) + M_0^{1-\sigma_1} e^{-\beta t} \right]^{1/(1-\sigma_1)} \tag{14}$$

From **Eq.14** it is found that, as $t \rightarrow \infty$, $m \rightarrow M_a$. It means that, after a sufficiently long time, the mass becomes almost equal to M_a . Practically, the organism does not appear to grow in size when its mass is very close to M_a .

Now using **Eqs.11** and **13** one may write the growth rate as

$$dm/dt = E_g = \left[C_1/C (1 - e^{-\beta t}) + M_0^{1-\sigma_1} e^{-\beta t} \right]^{\sigma_1/(1-\sigma_1)} \left[C_1 - C M_0^{1-\sigma_1} \right] e^{-\beta t} \tag{15}$$

Hence at $t = 0$, $dm/dt = C_1 M_0^{\sigma_1} - C M_0$. This is actually the initial growth rate and can also be obtained by putting $m = M_0$ in **Eq.11**. We have $dm/dt \rightarrow 0$ as $t \rightarrow \infty$. Thus, the growth rate never becomes exactly zero although no growth is practically observed after a certain age. After reaching the peak value, E_g decreases with time and, at a certain stage, it becomes too small to be practically measurable. From **Eq.11**, one can compute the mass (say M_g) for which E_g has its highest value. This mass corresponds to the fastest growth rate and it is expressed as

$$M_g = (C_1 \sigma_1 / C)^{1/(1-\sigma_1)} \tag{16}$$

Hence, the highest growth rate (E_{gM}) is given by

$$E_{gM} = E_g (at m = M_g) = C_1 (C_1 \sigma_1 / C)^{\sigma_1/(1-\sigma_1)} - C (C_1 \sigma_1 / C)^{1/(1-\sigma_1)} \tag{17}$$

Comparing M_g with M_{opt} in **Eq.6A**, we get $M_g < M_{opt}$, since $C_3 > 0$. It clearly implies that an organism attains the state of fastest growth before reaching the state of highest surplus power (E_s).

Eq.13 expresses mass as a function of time. The surplus power (E_s), being a function of mass, should also be a function of time. As m approaches its saturation value (M_a), E_s also approaches its saturation value (ε_s). Substituting $m = M_a$ in **Eq. 3** we get

$$\varepsilon_s = C_1 (C_1/C)^{\sigma_1/(1-\sigma_1)} - C_2 (C_1/C)^{1/(1-\sigma_1)} \tag{18}$$

Depending upon the growth parameters, there can be three different manners in which growth process can take place. These three possibilities are discussed below.

CASE 1:

The saturation mass (M_a) can be smaller than the optimum mass (M_{opt}). This case can be mathematically described as,

$$M_a < M_{opt} \Rightarrow C_3 > C_2 [(1 - \sigma_1) / \sigma_1] \tag{19}$$

The growth process, in this case, terminates before

reaching the state of optimum mass (M_{opt}). The saturation value (ε_s) of the surplus power is smaller than E_{sM} .

CASE 2:

$$M_a = M_{opt} \Rightarrow C_3 = C_2 \left[(1 - \sigma_1) / \sigma_1 \right]. \quad (20)$$

In this case, we have $\varepsilon_s = E_{sM}$ implying that after a sufficiently long time, the surplus power will almost remain at a constant level E_{sM} . As the growth process terminates the surplus power supply remains constant at its highest possible value. Therefore, the organism continues to live with the highest possible rate of surplus energy production.

CASE 3:

$$M_a > M_{opt} \Rightarrow C_3 < C_2 \left[(1 - \sigma_1) / \sigma_1 \right]. \quad (21)$$

Here the surplus energy saturates at a mass which exceeds the optimum mass. Then as like case1 we again have $\varepsilon_s < E_{sM}$. Here, E_s initially increases with time and after reaching the peak value (E_{sM}) it decreases to its saturation value (ε_s).

The conditions expressed by the **Eqs.19-21** can be expressed by a single relation

$$C_3 = \rho C_2 \left[(1 - \sigma_1) / \sigma_1 \right]. \quad (22)$$

For the above three cases we have, $\rho > 1$, $\rho = 1$ and $0 < \rho < 1$ respectively.

Using **Eqs.6A, 12** and **22** we define a quantity R as

$$R \equiv M_a / M_{opt} = \left(1 / (\sigma_1 + \rho(1 - \sigma_1)) \right)^{1/(1 - \sigma_1)} \quad (23)$$

This ratio (R) is a measure of the saturation mass relative to optimum mass. Since $\sigma_1 < 1$, we have $R \leq 1$ for $\rho \geq 1$ and $R > 1$ for $\rho < 1$. For $\rho \geq 1$, the energy allocation for growth process continues at most up to the optimum point. Beyond that point the surplus energy is allocated mainly for reproduction and other purposes. For $\rho < 1$, the energy allocation for growth continues beyond the optimum point and there is a gradual shift in energy allocation from growth process to that for reproduction. Using **Eqs.13** and **22** we get

$$m(t) = \left[C_1 \sigma_1 (1 - e^{-\beta t}) (C_2 (\sigma_1 + \rho(1 - \sigma_1))) + M_0^{1 - \sigma_1} e^{-\beta t} \right]^{1/(1 - \sigma_1)}, \quad (24)$$

where $\beta = C_2 (1 - \sigma_1) + (C_2 \rho / \sigma_1) (1 - \sigma_1)^2$.

Using the above expression of time-dependent mass, the surplus power (E_s) can be expressed as,

$$E_s = C_1 \left[A (1 - e^{-\beta t}) + M_0^{1 - \sigma_1} e^{-\beta t} \right]^{\sigma_1 / (1 - \sigma_1)} - C_2 \left[A (1 - e^{-\beta t}) + M_0^{1 - \sigma_1} e^{-\beta t} \right]^{1/(1 - \sigma_1)} \quad (25)$$

where $A = C_1 \sigma_1 / (C_2 (\sigma_1 + \rho(1 - \sigma_1)))$ and $\beta = C_2 (1 - \sigma_1) + (C_2 \rho / \sigma_1) (1 - \sigma_1)^2$. **Eq.25** shows how E_s , as a function of time, depends on the value of ρ .

Let us now define a time period T_λ as the time required for the organism to attain a mass m_λ where $m_\lambda = \lambda M_a$ and $0 < \lambda < 1$. Applying this definition and using **Eq.14** one may obtain

$$T_\lambda = 1 / (C(1 - \sigma_1)) \ln \left(\left(1 - (M_0 / M_a)^{1 - \sigma_1} \right) / (1 - \lambda^{1 - \sigma_1}) \right). \quad (26)$$

In **Eq.26**, it is evident that as σ_1 increases, more time is required to attain a certain fraction (λ) of the saturation mass (M_a). For organisms with higher values of σ_1 , the growth process continues for a longer time.

In the context of growth, one can define growth efficiency (ε_g) as the ratio of the amount of surplus energy used for growth to the total surplus energy available at the moment, and can be expressed as,

$$\varepsilon_g = E_g / E_s = 1 / E_s \cdot dm / dt = (C_1 m^{\sigma_1} - (C_2 + C_3) m) / (C_1 m^{\sigma_1} - C_2 m) \quad (27)$$

Since $dm/dt \rightarrow 0$ as $t \rightarrow \infty$, we must have $\varepsilon_g \rightarrow 0$ as $t \rightarrow \infty$.

In a similar fashion, one can define the reproduction efficiency (ε_p) as the ratio of the amount of surplus energy used for reproduction to the total surplus energy available at the moment, and it can be expressed as

$$\varepsilon_p = 1 - \varepsilon_g = C_3 m / (C_1 m^{\sigma_1} - C_2 m). \quad (28)$$

As $t \rightarrow \infty$, $\varepsilon_g \rightarrow 0$ and therefore $\varepsilon_p \rightarrow 1$.

It is consistent with the practical observation that, as mass increases the proportion of energy allocation for growth decreases and the energy allocation for reproduction increases.

The rate of change of growth and reproduction efficiencies with respect to mass can be expressed as

$$d\varepsilon_p / dm = -d\varepsilon_g / dm = C_1 C_3 m^{\sigma_1} (1 - \sigma_1) / (C_1 m^{\sigma_1} - C_2 m)^2 \quad (29)$$

Since $\sigma_1 < 1$, the right hand side of **Eq.29** is a positive quantity. Therefore, as mass increases, ε_p continues to increase and ε_g continues to decrease. **Eq.29** suggests that, under no circumstances, $d\varepsilon_p / dm$ and $d\varepsilon_g / dm$ can be equal to zero. As a result one concludes that an organism, in its life span, never attains a mass for which its reproduction (or, growth) efficiency would be a maximum. In different organisms the growth efficiency seems to have a universal dependence on relative body mass [31,32]. Using the small amount of available data, Makarieva et al. [27] has concluded that there is a negative correlation between growth efficiency and metabolic

rate. So the conclusion, drawn from Eq.28 is in good agreement with the literature in this topic.

The time taken by the organism to reach the state of highest growth rate can be determined by substituting $m = M_g$ in Eq.13 from Eq.16. This span of time, denoted by T_h is

$$T_h = \beta^{-1} \ln \left[(C_1 \sigma_1 / C - C_1 / C)^{-1} (M_0^{1-\sigma_1} - C_1 / C) \right] \tag{30}$$

$$= \beta^{-1} \ln \left[(\sigma_1 - 1)^{-1} (M_a^{\sigma_1 - 1} M_0^{1 - \sigma_1} - 1) \right]$$

A Special Case: Length-Biomass Allometry

In our recent study of length-biomass allometry of bi-dimensional seaweeds we have shown that the variation of length with time can be described properly in terms of two length parameters perpendicular to each other [33]. These are actually the sides of the smallest rectangle that can enclose the organism. This theoretical analysis was made in an attempt to explain the experimental findings of Scrosati on flat seaweeds [34]. According to this theoretical model, these two length parameters (say L_1 and L_2) has a power-law relation between them. This relation is given by,

$$L_2 = k(L_1)^\lambda \tag{31}$$

Here, k is a constant of proportionality. From experimental observations, an average estimate of λ was found to be 1.119 for the organisms described in our article [33]. These length parameters, L_1 and L_2 , have separate allometric relations with the mass of the organism. In the present article we have explored the mass-time relationship. Therefore, one can now formulate the length-time relationship of such species.

For the species of bi-dimensional seaweeds described in that article [33], an average estimate of the length-biomass allometry can be expressed by the following equations.

$$L_1 = 7.811 m^{0.472} \tag{32A}$$

$$L_2 = k(L_1)^\lambda = 9.976 k m^{0.528} \tag{32B}$$

The mass (m) in the above equations is a function of time and its variation with time is described by the Eqs. 13 and 14 of the present study. It is a common observation that growth does not take place identically along two perpendicular directions in any flat organism. From the above equations the rates of growth along these directions can be expressed as

$$dL_1/dt = 3.687 m^{-0.528} dm/dt \tag{33A}$$

$$dL_2/dt = 5.267k m^{-0.472} dm/dt \tag{33B}$$

Here, dm/dt is a function of time. Its dependence on

time is expressed by Eq.15 of the present study.

3. GRAPHICAL DEPICTION AND ANALYSIS

Using the expressions derived in this article, we have illustrated various growth features graphically.

Figure 1 shows the general nature of dependence of mass (m) and growth rate (dm/dt) on time. These graphs are based on the Eqs.13 and 15. The mass initially increases rapidly with time and, after a sufficiently long time, it becomes asymptotic to the value of M_a . The rate of growth (dm/dt) has a very sharp rise at the initial stage and, after reaching its peak value, it decreases slowly, becoming negligible after a sufficiently long time. As $t \rightarrow \infty$, we have $m \rightarrow M_a$ and $dm/dt \rightarrow 0$. This figure shows that the growth process never stops but it becomes so slow that it does not remain perceptible after a certain point of time (such as, at nearly $t = 5$ in Figure 1).

Figure 2 shows the variation of growth rate as a function of mass for different values of the scaling exponent σ_1 . For higher values of σ_1 , the growth rate is higher and the duration of growth process is longer. At the very initial stage of growth, the rise in growth rate is almost independent of σ_1 . The time required for attaining the peak rate is longer for higher values of σ_1 . After reaching the peak value, the growth rate decreases but it does not fall as rapidly as it rises at the initial stage.

The graphs in Figure 3 show the change of mass of an organism with time for different values of the constant C_1 . As time goes on, the mass (m) becomes closer and

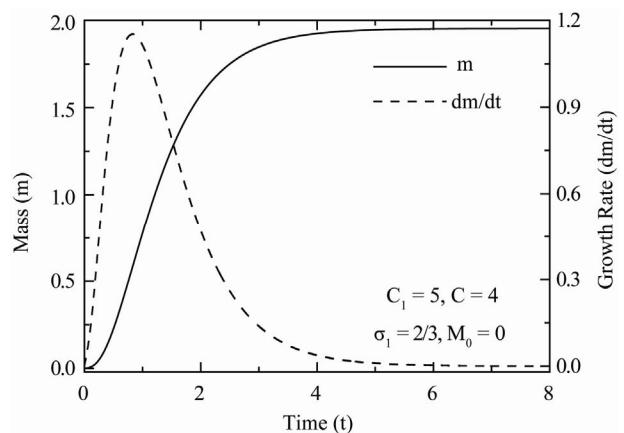


Figure 1. It shows the variation of mass and growth rate as functions of time. Here, the mass increases with a gradually decreasing rate and finally it becomes asymptotic to the value of M_a . The rate of growth rises fast at the initial stage; reaches its peak value and then continues to decrease slowly. At $t \rightarrow \infty$, we have $m \rightarrow M_a$ and $dm/dt \rightarrow 0$. In this case the value of M_a is 1.953. The growth rate reaches its highest value at $m = M_g = 0.579$.

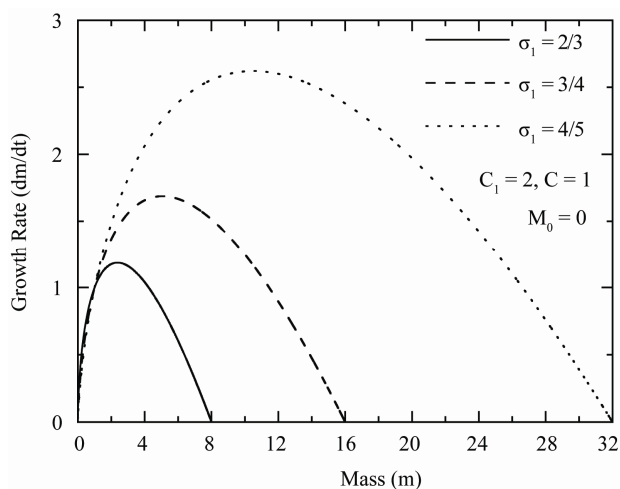


Figure 2. These plots show the change of the growth rate with mass for different values of the scaling exponent σ_1 . For higher values of σ_1 , the growth process continues for a longer time and the growth rate becomes higher. At the very initial stage of growth, the rise in growth rate seems to be almost independent of σ_1 . As σ_1 increases, the time required for attaining the peak rate increases. After reaching the peak value, the growth rate decreases but it does not fall as rapidly as it rises at the initial stage. The values of M_g for these three cases are 2.370, 5.063 and 10.486.

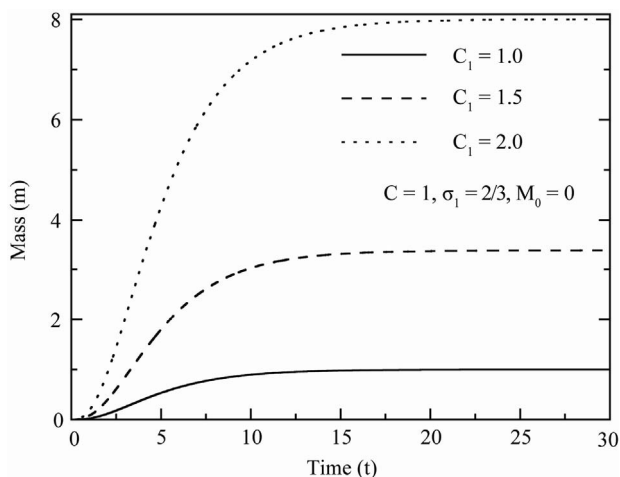


Figure 3. These plots show how the mass of an organism increases with time for different values of the constant C_1 . The mass (m) approaches a saturation level (M_a) which increases with a rise in C_1 . After a certain point of time the rise in mass becomes so slow that practically no growth can be observed. The values of M_a for these three cases are 1, 3.375 and 8.

closer to its saturation level (M_a) which increases with a rise in C_1 . After a long time the mass changes so slowly that no growth can be practically observed. The values of M_a for these three cases are 1, 3.375 and 8. These values are consistent with Eq.12, according to which, M_a increase as the ratio C_1/C and σ_1 become larger.

The graphs in Figure 4 show the dependence of

growth rate on time for different values of the constant C_1 . It is evident from these graphs that the time required for attaining the peak growth rate is independent of C_1 . For higher values of this constant, the growth rate is higher at any stage of the growth process. The change in mass remains perceptible until dm/dt becomes negligible. This effective termination point of growth is found to be the same for the cases shown in this figure and in Figure 3. Therefore, the effective duration of growth process is independent of C_1 .

Figure 5 shows the dependence of growth rate on time for different values of the constant C . As C increases, the growth rate becomes smaller and the effective duration of growth process becomes shorter. It is found in these graphs that, as C increases, the time to reach the peak rate becomes shorter. According to Eqs.13 and 15, as C increases, the value of β increases and hence the organism approaches the effective termination point faster.

Figure 6 shows the variation of growth rate with time for different values of the scaling exponent σ_1 . For higher values of σ_1 , the effective duration of growth process is longer. At the very early stage of growth, an organism with smaller value of σ_1 has greater growth rate. Apart from this stage, organisms with higher values of σ_1 have larger growth rates in general. An organism with larger value of σ_1 takes more time in attaining the peak growth rate.

The variation of surplus power with time, for different values of the ρ , is shown in Figure 7. For $\rho = 1$, E_s

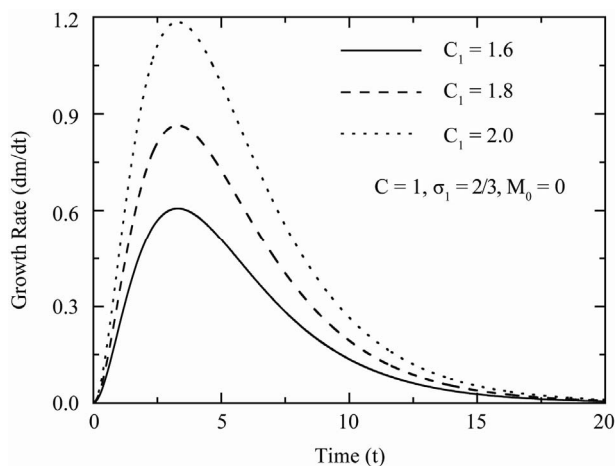


Figure 4. This figure shows the variation of growth rate with time for different values of the constant C_1 . For higher values of this constant, the growth rate becomes higher at any stage of the growth process. For these three cases, the growth rates attain their respective peaks at the same time. The increase in mass remains perceptible up to a certain point where dm/dt is almost zero. This effective termination point of growth is found to be the same for the cases shown in this figure. Thus, the effective duration of growth process is independent of C_1 .

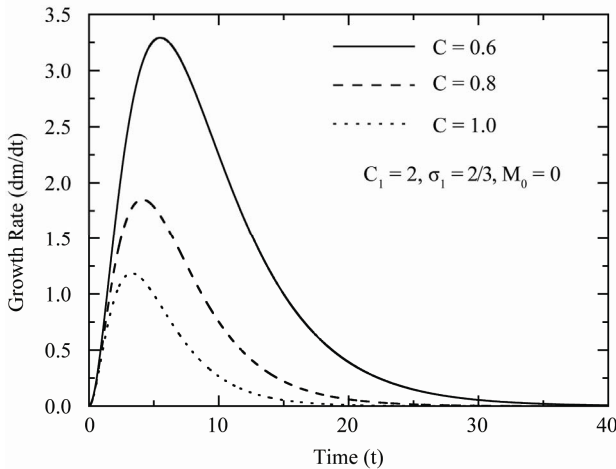


Figure 5. These plots show the variation of growth rate with time for different values of the constant C . For higher values of this constant, the growth process becomes slower at any stage of the growth process. It is evident from the graphs that as C increases, the time required for attaining the peak rate becomes shorter. The increase in mass remains perceptible up to a certain point where dm/dt is almost zero. For higher values of C , the organism approaches this effective termination point with greater rapidity. Thus, the effective duration of growth process becomes shorter for higher values of C .

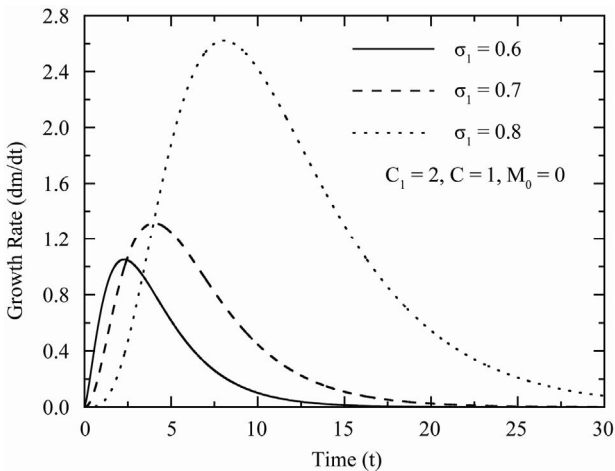


Figure 6. This figure shows the variation of growth rate with time for different values of the scaling exponent σ_1 . It is clearly evident from these graphs that, as σ_1 increases, the effective duration of growth process increases. At the very early stage of growth, an organism with smaller value of σ_1 has greater growth rate. Except for this very small period, growth rate is higher for larger values of σ_1 . For higher values of σ_1 , the organism takes more time to attain the state of largest growth rate.

tends to reach the highest possible surplus power (E_{sM}), implying that the organism continues to live with the largest supply of surplus power. For $\rho < 1$, E_s initially increases with time, reaches the peak value at $m = M_{opt}$ and, beyond that point, it attains saturation at a level

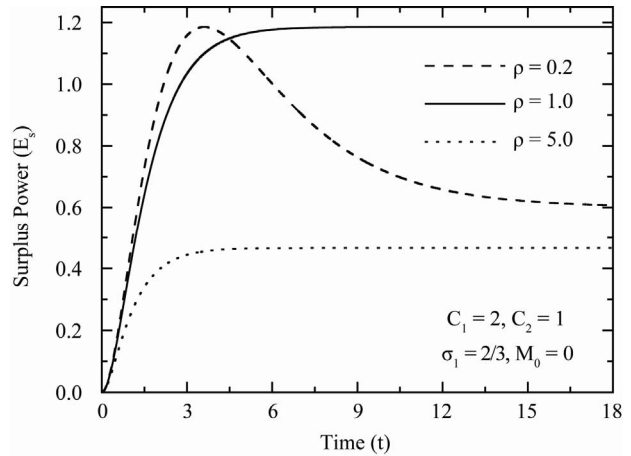


Figure 7. This figure shows the variation of surplus power with time for different values of the constant ρ . For $\rho = 1$ we have $M_a = M_{opt}$, for $\rho < 1$ we have $M_a > M_{opt}$ and for $\rho > 1$ we have $M_a < M_{opt}$. For $\rho = 1$, the saturation value of E_s is equal to the highest possible surplus power (E_{sM}). For $\rho < 1$, E_s initially increases with time, reaching its peak value (E_{sM}) at $m = M_{opt}$ and then decreases to saturate at a level smaller than E_{sM} . For $\rho > 1$, the mass saturates at a level smaller than M_{opt} and consequently, E_s saturates at a level smaller than E_{sM} .

smaller than E_{sM} . For $\rho > 1$, the mass attains its saturation level before reaching the value of M_{opt} and therefore, E_s saturates at a level smaller than E_{sM} .

Figure 8 shows the change of growth efficiency (ϵ_g) and reproduction efficiency (ϵ_p) with respect to the ratio m/M_a , which is actually a measure of mass relative to its saturation value. As the growth process proceeds towards completion, this ratio (m/M_a) approaches unity. This ratio, therefore, is a measure of the degree of completion of the growth process in an organism. As growth continues, ϵ_g decreases from 1 to 0 and ϵ_p increases from 0 to 1. With a rise in mass, the utilization of surplus energy for reproduction increases and its allocation for growth decreases.

Figure 9 show the variation of growth efficiency with time for different values of the constant ρ . At $t = 0$, the efficiency has the highest value (*i.e.* unity), for any value of ρ . The growth efficiency decreases with time and it approaches its lowest value (*i.e.* zero) as $t \rightarrow \infty$, for any value of ρ . As ρ increases, the growth efficiency decreases faster with time. For higher values of ρ , the growth efficiency is smaller at any stage of the growth process. Thus, for larger values of ρ , the utilization of surplus energy for growth is smaller.

Figure 10 shows the variation of T_λ as a function of λ , for different values of the scaling exponent σ_1 . For any value of λ , T_λ is larger for higher values of σ_1 . Near the right edge of the above frame, a vertical line has been drawn to mark the point where the mass attains 95% of its saturation level (M_a). Near this point, the

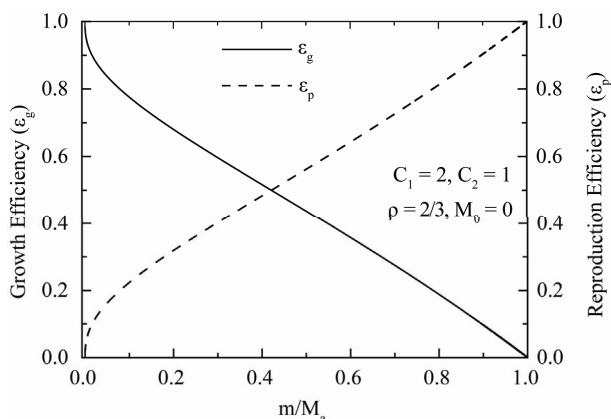


Figure 8. This figure shows the variations of growth efficiency (ϵ_g) and reproduction efficiency (ϵ_p) with respect to the ratio m/M_a . As the growth process approaches termination, this ratio (m/M_a) approaches unity. As growth continues, ϵ_g decreases from 1 to 0 and ϵ_p increases from 0 to 1. With a rise in mass, the utilization of surplus energy for reproduction increases and its allocation for growth decreases.

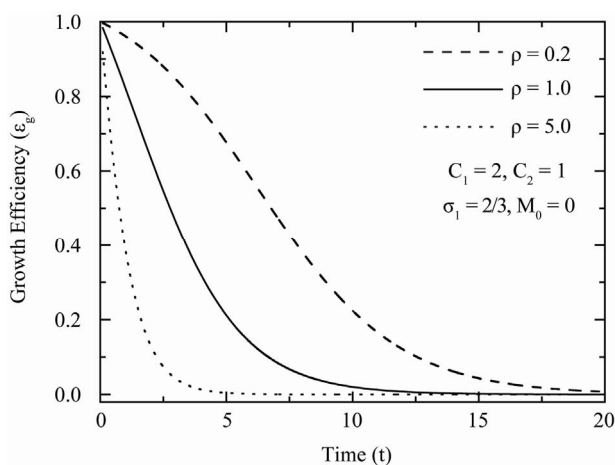


Figure 9. These graphs show the variation of growth efficiency with time for different values of the constant ρ . At $t = 0$, the efficiency has the highest value (*i.e.* unity), irrespective of the value of ρ . The growth efficiency is found to decrease with time and it approaches its lowest value (*i.e.* zero) as $t \rightarrow \infty$ in all these three cases. As ρ becomes larger, the growth efficiency falls more rapidly with time. For higher values of ρ , the growth efficiency is smaller at any stage of the growth process. Thus, for larger values of ρ , smaller fraction of surplus energy is utilized for growth.

slopes of these curves become extremely high, implying the fact that a very long time is required for a slight change in mass. This vertical line almost marks the effective termination point of growth because any practical observation (or measurement) of growth becomes more and more difficult at this stage.

Figure 11 shows the variation of the length parameters (L_1 and L_2) of a bi-dimensional organism with time. These plots are based on the **Eqs.32A** and **B** for L_1

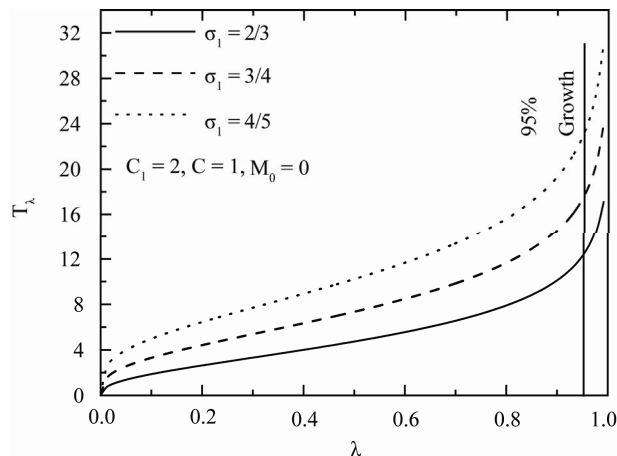


Figure 10. This figure shows the variation of T_λ as a function of λ , for different values of the scaling exponent σ_1 . For any value of λ , T_λ is larger for higher values of σ_1 . The vertical line, near the right edge of the frame, mark the point where $m = 0.95 M_a$. Very high slope near this point implies that practically very little rise in mass is observable at this stage of the growth process.

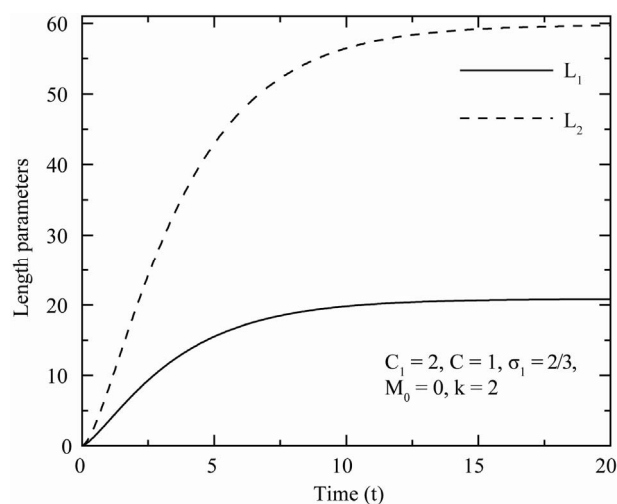


Figure 11. This figure shows the variation of the length parameters (L_1 and L_2) of bi-dimensional organisms with time. One of the parameters attains the state of saturation earlier than the other.

and L_2 respectively. Here, the time dependence of mass (m) has been obtained from **Eq.13**. One of the parameters attains the state of saturation earlier than the other, which is quite consistent with our observations.

Figure 12 shows the rate of change of two length parameters of a bi-dimensional organism as functions of time. These plots are based on the **Eqs.33A** and **B** for L_1 and L_2 respectively. Here, the time dependence of the growth rate (dm/dt) has been obtained from **Eq.15**. Any of these rates attains a maximum value and then decreases to zero asymptotically. One of the rates attains peak value earlier and goes to zero faster than the other

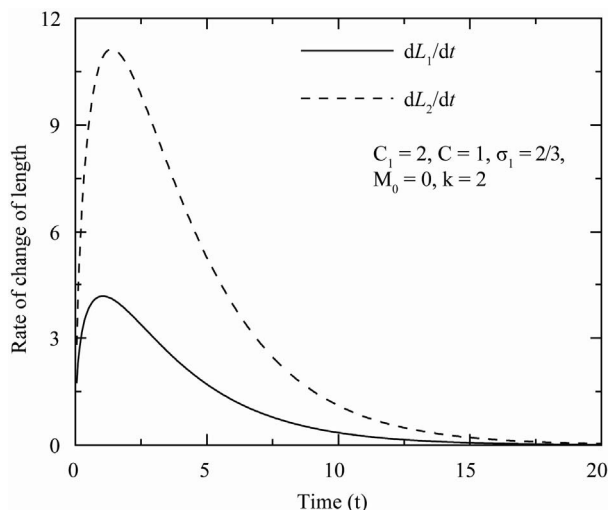


Figure 12. This figure shows the rate of change of two length parameters of bi-dimensional organisms as functions of time. The rate attains a maximum value and then decreases to zero asymptotically. One of the rates attains peak value earlier and goes to zero faster than the other parameter.

parameter.

An important fact, regarding the constant C_3 , comes out in this growth model. Using **Eqs.6A** and **11** it is found that, at $m = M_{opt}$ this constant is given by

$$C_3 = -dE_g/dm = -d/dm (dm/dt). \quad (34)$$

Using **Eq.34**, one can determine the value of C_3 experimentally.

4. CONCLUSIONS

An organism must always have some surplus energy (E_s) for a healthy survival which involves processes like repair, maintenance and coping with environmental fluctuations etc. apart from growth and reproduction phenomena. Therefore, the net amount of surplus energy or the mass specific surplus energy may be the determining factors for mortality of an organism. For such quantities, there should be specified limit below which the survival of the organism is not possible and the limiting value may be different for different species. Generally, a part of surplus energy is always converted into mass, causing an enhancement in size of the organism. There should be an extensive experimental investigation to find out the functional dependence of reproduction (or, growth) efficiency on body mass. Through the present mathematical formulations, we have shown that biological growth process can take place in three possible modes, depending on the relationships among various parameters. Using this model, we have analyzed the mechanism of variation of length with age of a bi-dimensional organism where growth takes place essentially along two dimensions. The

usefulness of this model is that, using the expressions of M_a , M_g , T_λ , T_h it would be possible to determine the values of σ_1 , C_1 , C_2 and C_3 from experimental observations, leading to a deeper insight into the energy allocation for different physiological purposes.

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