

Role of Rate of Specific Growth Rate in Different Growth Processes: A First Principle Approach

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Abstract

In the present communication, effort is given for the development of a common platform that helps to address several growth processes found in literature. Based on first principle approach, the role of rate of specific growth rate in different growth processes has been considered in an unified manner. It is found that different growth equations can be derived from the same rate equation of specific growth rate. The dependence of growth features of different growth processes on the parameters of the rate equation of specific growth rate has been examined in detail. It is found that competitive environment may increase the saturation level of population size. The exponential growth could also be addressed in terms of two important factors of growth dynamics, as reproduction and competition. These features are,

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most probably, not reported earlier.

Keyword:

Specific growth rate, Growth equation, Kleiber law of growth, Generalized logistic growth, Potential growth.

1 Introduction

Growth, an extremely complex and nonlinear phenomenon observed in the field of biology, economics and other natural sciences, is drawing attention of researchers over the century. Several models have been developed in order to describe growth of biological systems. These models, discrete or continuous by nature, are introduced mostly to describe population dynamics. Others are used to describe the growth a physical quantity of interest.

The exponential growth model, treated as one of the simplest model, can describe approximately such growth for the initial period. According to this model, the population will continue to increase as no intra or interspecific competition is considered. It may continue to decrease if an initial growth reduction factor is a part of the system. Even this model does not consider the limitation of resources imposed by the environment. Such growth model is unrealistic to describe a biological system. Through it is observed in different physical systems, i.e; autocatalytic reaction, radioactive decay, bacterial cloning [1] etc.

Potential growth, other than exponential growth, also shows non-saturated growth and does not reach carrying capacity. It is direct consequence of a complex system where different level of the system have direct consequence on growth [2]. Potential growth function is extensively used in different fields of application [3, 4, 5, 6, 7].

Logistic growth model, in continuous [8, 9] or discrete [10] form, includes the initial exponential nature of growth rate and competition under limited resources described by saturation values. Discrete logistic growth equations are able to describe chaotic behaviours of the system [11]. The continuous form of logistic growth models do not show intrinsic bifurcations, and as a result, it is much more easier to handle analytically. The inflection point of such model is fixed and always takes place at the population size that is half of the saturation value. This imposes undesirable restriction on the shape of the characteristic curve. Though, it forms the basis of several extended models [12, 13, 14]. Logistic growth model is extensively used in the field of

biology [15, 16, 17] and outside the field of biology [18, 19, 20].

A slightly generalized version of the logistic growth model, termed as generalised logistic growth model or θ -logistic growth model, is also introduced to study plant growth [21, 22], population ecology [23, 24], avian population dynamics [25], environmental stochasticity on population growth [26], species abundance in community ecology [27]. Similar to logistic growth model, the population in this type of growth model converges with time to the same saturation level. In this model, a new parameter (θ) representing intra-specific competition regulates the time required to reach its saturation value, may be termed as carrying capacity.

The growth model showing saturated nature other than logistic and generalized logistic growth model are von Bertalanffy model [28, 29], Kleiber law of growth [30], Gompertzian growth [31] etc. von Bertalanffy model is frequently used in different types of allometric modelling. In this type of growth, energy consumed by an organism is considered to be proportional to the surface area of the body of an organism. Kleiber law of growth is recently successfully used by West *et al.* [32] to derive a differential equation showing growth of biological masses. They have considered fractal like branching of network for the transportation of resources. Gompertz growth model, formulated to model human demographic data, is also frequently used in modelling tumour growth [33].

The analysis and comparison of different types of growth model in a unified manner is expected for better understanding of growth processes. Tsoularis *et al.* [14] tried to address this issue by proposing generalized logistic growth model, but the proposed form of generalized growth model is empirical. They have shown that different types of growth models can be derived as a special case of their proposed functional form. Castorina *et al.* also tried to address Gompertz and West-type growth in terms of adimensional analysis [34]. They have failed to describe logistic growth ([35]).

In the present communication, different types of growth models mentioned above are addressed from first principle approach that is not empirical by nature. Different functional form of growth equation have been treated from the viewpoint of the rate of specific growth rate. It is shown that different growth models mentioned above can be derived from the same rate equation of specific growth rate. Generally, the rate of specific growth rate is zero (in other word, specific growth rate is a constant quantity) for exponential growth. It is also found in this study that the proposed rate equation of specific growth rate with specified condition leads to exponential growth. It

is most probable that we are going to report such behaviour for the first time. This finding may be helpful for the researchers for the better understanding of a growing system showing exponential growth. It is also found that a competitive environment may be responsible for increase in population size. In this connection, the variation in growth features of different growth processes has been studied in terms of different parameters involved in first principle approach.

The paper is organized as follows: In Sec. II, we first propose a description of a growing system based on first principle approach. Here we consider a specified form of rate equation of specific growth rate. Then we have shown that different types of growth equation can be addressed from the same rate equation of specific growth rate. In sec. III, we consider the dependence of growth features of different growth processes on the parameters of the proposed description. We show in this section that one of the factors responsible for increase in population size may be competitive environment. A possible explanation of parameters involved in the description of growth processes is given in terms of reproduction processes and energy consumption of a growing system. Finally we conclude about our result in section IV.

2 The Role of Specific Growth Rate in Different Growth Processes

Growth in a physical process may be addressed by two state variables, which are (i) the observed physical quantity (x) of interest, and (ii) the specific growth rate (s) of the physical quantity (x). Therefore, growth or evolution of any physical quantity (x) with time (t) in a physical process can be expressed in the following form,

$$\frac{dx}{dt} = s(t)x(t) \quad (1)$$

Where, $s(t)$ is the specific growth rate of the variable $x(t)$. It is expected that the rate of change of specific growth rate (i.e, \dot{s}) must be less than zero to reach a saturation level of the growth process. Therefore,

$$\frac{ds}{dt} < 0 \quad (2)$$

Hence, it would be better to introduce a variable $R(s)$ that can be expressed as,

$$R(s) = -\frac{ds}{dt} \quad (3)$$

$R(s)$ can be expressed in terms of power series as,

$$R(s) = \sum_0^{\infty} p_n s^n \quad (4)$$

When $R(s) = p_1 s + p_2 s^2$, x can be expressed as,

$$x = \left[\frac{x_0^2(p_1 + p_2 s_0)}{p_1} - \frac{x_0^2 p_2 s_0}{p_1 \exp(p_1 t)} \right]^{\frac{1}{p_2}} \quad (5)$$

and, growth rate ($\frac{dx}{dt}$) can be expressed as

$$\frac{dx}{dt} = \frac{x_0^2(p_1 + p_2 s_0)}{p_2} x^{1-p_2} - \frac{p_1}{p_2} x \quad (6)$$

Where, x_0 and s_0 are two constants defined as $s = s_0$ and $x = x_0$ at $t = 0$. Now, we reconsider some well known growth forms and establish that they could all be derived from equation (6).

2.1 Exponential growth

It is well known fact that the specific growth rate is a constant quantity for exponential growth. In other word, the rate of change of specific growth rate is zero (means $R = 0$). For this condition, the physical quantity (x) can be expressed as,

$$x = x_0 \exp(s_0 t) \quad (7)$$

But it can be shown that equation (6) takes the the following form for the condition $p_1 + p_2 s_0 = 0$ as,

$$\frac{dx}{dt} = -\frac{p_1}{p_2} x \quad (8)$$

Then, the state variable (x) of equation (17) can be expressed as,

$$x = x_0 \exp(s_0 t) \quad (9)$$

It shows exponential growth of the physical quantity x .

2.2 Logistic growth and θ - logistic growth

When $p_2 < 0$, say $p_2 = -\beta$, equation (6) can be expressed as,

$$\frac{dx}{dt} = \frac{p_1}{\beta} x \left[1 - \frac{x^\beta}{\frac{x_0^\beta p_1}{p_1 - \beta s_0}} \right] \quad (10)$$

When $p_1 - \beta s_0 \neq 0$, equation (10) can be expressed as,

$$\frac{dx}{dt} = \frac{p_1}{\beta} x \left[1 - \frac{x^\beta}{K^\beta} \right] \quad (11)$$

Where, $\frac{x_0^\beta p_1}{p_1 - \beta s_0} = K^\beta$. It is the form of θ -logistic growth [22]. It shows more accurate results than usual logistic growth [23].

When $\beta = 1$ or $p_2 = -1$, equation (11) can be expressed in form of usual logistic growth as,

$$\frac{dx}{dt} = p_1 x \left[1 - \frac{x}{K} \right] \quad (12)$$

2.3 Gompertz law of growth

Equation (11) can be expressed as,

$$\frac{dx}{dt} = \frac{p_1}{\beta} x \left[1 - \exp \left(\beta \ln \frac{x}{K} \right) \right] \quad (13)$$

$$= p_1 x \left[-\ln \frac{x}{K} - \beta \left(\ln \frac{x}{K} \right)^2 \right] \quad (14)$$

When $\beta \rightarrow 0$, equation (14) can be expressed as,

$$\frac{dx}{dt} = p_1 x \ln \frac{K}{x} \quad (15)$$

Equation (15) represents Gompertz law of growth. It was first introduced to evaluate mortality table [31]. It is also frequently used for the description of tumour growth [36, 37].

2.4 Potential growth law

From equation (6), it can be shown that $\frac{dx}{dt} \rightarrow x_0^2 s_0 x^{1-p_2}$ when $p_1 \rightarrow 0$. The physical quantity (x) can be expressed for this condition as,

$$x \rightarrow (x_0^{p_2} + x_0^2 s_0 p_2 t)^{\frac{1}{p_2}} \quad (16)$$

It represents potential growth function used in tumour biology [3], lifehistory theory [4], early-life evolution [2].

It leads to linear growth with time for the conditions: $p_1 \rightarrow 0$ and $p_2 = 1$.

2.5 von Bertalanffy and Keblier law of growth

When $0 < p_2 < 1$ and $p_2 = 0.34$, equation (6) can be expressed as,

$$\frac{dx}{dt} = \alpha_1 x^{0.66} - \alpha_2 x \quad (17)$$

Where, $\alpha_1 = \frac{x_0^2(p_1+0.34s_0)}{0.34}$ and $\alpha_2 = \frac{p_1}{0.34}$.

This is known as von Bertalanffy growth equation introduced to model fish weight growth [38]. It is based on a simple assumption that the energy consumed by an organism is proportional to the surface area of the body of that organism. It is basically a modification of Verhulst logistic growth and can be treated as a special case of Bernoulli differential equation.

Again, equation (6) can be expressed for $p_2 = 0.25$ as,

$$\frac{dx}{dt} = \alpha_1 x^{0.75} - \alpha_2 x \quad (18)$$

Where, $\alpha_1 = \frac{x_0^2(p_1+0.25s_0)}{0.25}$ and $\alpha_2 = \frac{p_1}{0.25}$.

This is Keblier law of growth that is successfully used by West *et al.* to describe the evolution of biological masses [32]. They have considered fractal-like distribution of resources in a living organism. The ontogenetic growth model proposed by West *et al.* can successfully describe the growth of any living organism, from protozoa to mammals.

Conditional evolution of different growth equations from the proposed rate equation of specific growth rate is presented in table 1.

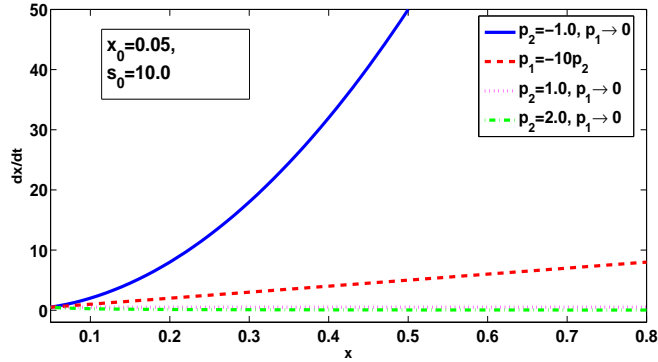


Figure 1: (Colour online) Plots of growth rate with respect to state variable x with $x_0 = 0.05$ and $s_0 = 10$ for $R = p_1 s + p_2 s^2$. From the top, the values of the parameter p_2 are -1.0 (potential growth for $p_1 \rightarrow 0$), $p_2 = -p_1/10$ (exponential growth), 1.0 (linear growth for $p_1 \rightarrow 0$) and 2.0 (potential growth for $p_1 \rightarrow 0$) respectively.

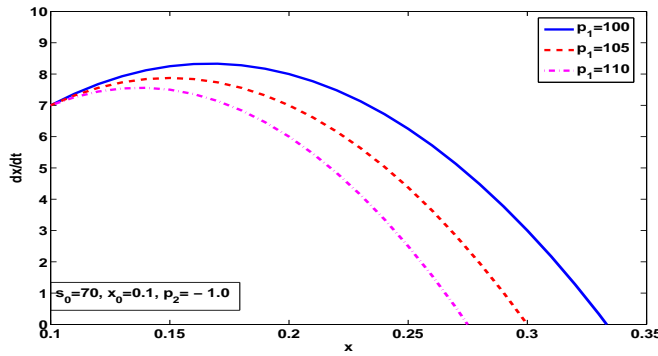


Figure 2: (Colour online) Plots of growth rate with respect to state variable x with $x_0 = 0.1$, $s_0 = 70$ and $p_2 = -1$ for $R = p_1 s + p_2 s^2$. From the top, the values of the parameter p_1 are 100, 105 and 110 respectively. All of them represent usual logistic growth by nature.

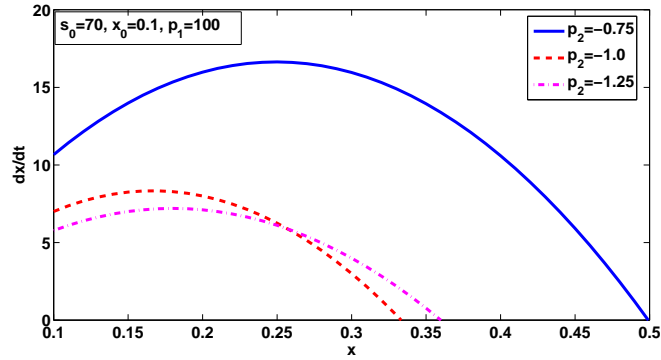


Figure 3: (Colour online) Plots of growth rate with respect to state variable x with $x_0 = 0.1$, $s_0 = 70$ and $p_1 = 100$ for $R = p_1 s + p_2 s^2$. From the top, the values of the parameter p_2 are -0.75 , -1.0 and -1.25 respectively. Second from the top represents usual logistic growth. Others are θ -logistic growth by nature.

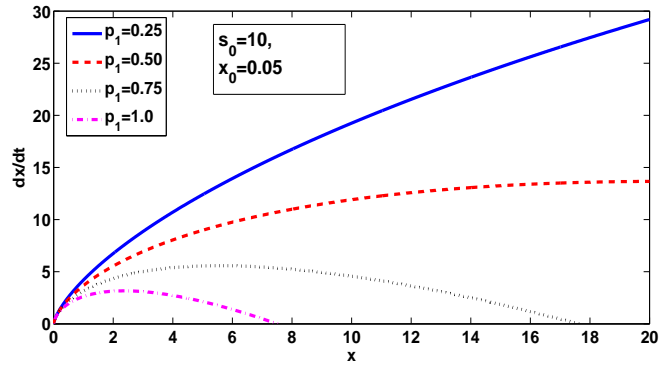


Figure 4: (Colour online) Plots of growth rate with respect to state variable x with $x_0 = 0.05$, $s_0 = 10$ and $p_2 = 0.25$ for $R = p_1 s + p_2 s^2$. From the top, the values of the parameter p_1 are 0.25 , 0.5 , 0.75 and 1.0 respectively. All of them represent West-type biological growth processes.

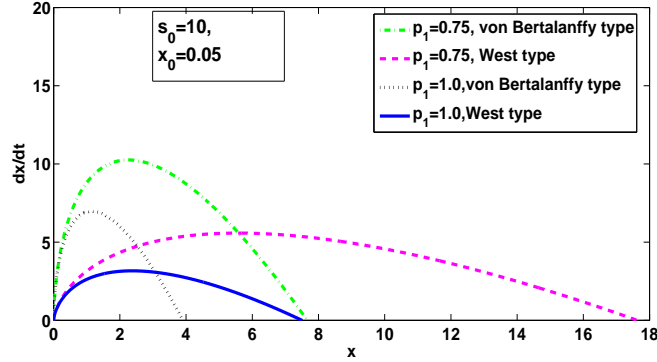


Figure 5: (Colour online) A comparative representation of von Bertalanffy type and West type growth for the same p_1 in terms of plots of growth rate with respect to state variable x with $x_0 = 0.05$, $s_0 = 10$ for $R = p_1 s + p_2 s^2$. First and third from the top represent von Bertalanffy type growth ($p_2=0.34$) for $p_1 = 0.75$ and $p_1 = 1.0$ respectively. Second and fourth from the top represent West type growth ($p_2=0.25$) for the same p_1 .

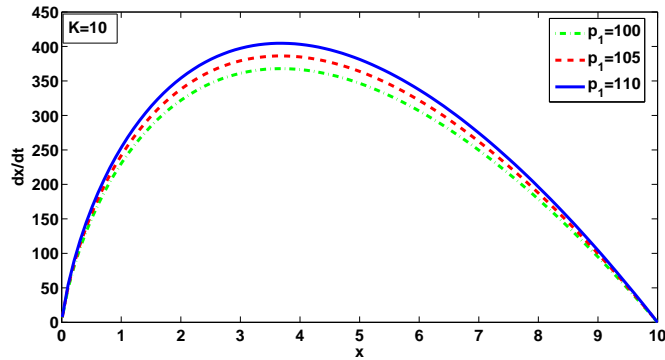


Figure 6: (Colour online) Plots of growth rate with respect to state variable x with $K = 10$ and $p_2 \rightarrow 0$ for $R = p_1 s + p_2 s^2$. From the top, the values of the parameter p_1 are 110, 105 and 100 respectively. All of them represent Gompertzian growth by nature.

Table 1: Conditional evolution of different growth functions from same rate equation of specific growth rate.

Rate of specific growth rate	Initial values of state variables	Conditions	Nature of growth
$p_1s + p_2s^2$	$s_0 > 0$ $x_0 > 0$	$p_1 > 0, p_2 \rightarrow 0, p_1 + s_0p_2 > 0$	Gompertzian
		$p_1 + s_0p_2 = 0$	Exponential
		$p_1 \rightarrow 0, p_2 > 0$	Potential
		$p_1 > 0, p_2 = -1, p_1 + s_0p_2 > 0$	Logistic
		$p_1 > 0, p_2 < 0, p_1 + s_0p_2 > 0$	θ -logistic
		$p_1 > 0, p_2 = 0.25, p_1 + s_0p_2 > 0$	West-type, Keblier
		$p_1 > 0, p_2 = 0.34, p_1 + s_0p_2 > 0$	von Bertalanffy
		$p_1 \rightarrow 0, p_2 = 1.0$	Linear

3 Discussions

The first principle approach proposed here is enriched with several quantitative solutions related to growth mechanisms often found in literature. It ranges from cancer and ontogeny, cellular populations in eucariots, to community ecology, to population biology of mammals and birds. It is useful to represent different types of sigmoidal growth and non-sigmoidal growth. It is expected that the state variable (x) must reach a saturation level (x_{max}) for different types sigmoidal growth for which $x_{max} > 0$ and $s = 0$. To satisfy these conditions, the following condition must be obeyed by the growing system,

$$p_1 > -p_2s_0 \quad (19)$$

Environmental changes and adoptive strategies are well-known to unbalance equilibrium of a population. As a result of such perturbation, a change in p_1 and/or p_2 of the system is expected. The system then would try to reset its saturated value (governed by the value of p_1 and p_2) to a new level and it would show growth (or decay) to attain that level. If the perturbation is very high, the system will follow a new growth dynamics based on the value of p_1 and p_2 . such deviation from saturated level and attainment of new saturation level could be explained by means of an unified approach for different growth mechanisms. The basis of such unified approach proposed here based on first principle approach is rate equation of specific growth rate. Therefore, it is possible to address attainment of different saturation levels

by a growing system at different instant of time.

In the following sections, we should consider the effect of variation of parameters related to different growth processes and a possible interpretation of a growth process based on the same rate equation of specific growth rate.

3.1 Potential Growth

Potential growth is found to be observed in different physical system [3, 4, 6]. It could be considered as one of the limiting case of the rate equation of specific growth rate represented by $\frac{ds}{dt} = -(p_1s + p_2s^2)$. According to this proposed description, it depends on only p_2 . As a result, it can be concluded that only one type of growth mechanism is dominant in this type of growing system. The growth rate may be slower or faster than that of exponential process, based on the magnitude of p_2 . It is represented by first and forth characteristic line, from the top, of figure 1. The third characteristic line from the top of figure 1 represents linear growth ($p_2 = 1.0$). According to this proposition, it can be treated as a special case of potential growth.

The main issue of lifehistory theory is the allocation of energy consumed by an organism for different types of adaptive strategies in distinct stages of life. Reproduction and survival are important factors in determining growth of an organism [4]. Consumed energy is mainly used for growth in non-reproductive stage of the organism. At this stage, the allocation of consumed energy depends on the size of the organism and follows a potential growth function [4]. The allocation of energy for reproduction is negligible ($p_1 \rightarrow 0$). Less amount of energy is allocated for growth when reproduction gains profound importance. The consumed energy is then distributed between survival and reproduction. The value of p_2 may be related to the strategy of partitioning of energy consumed by the organism between survival and growth. Therefore, it may be concluded from the above consideration that the parameter p_1 may be related to reproduction processes whereas p_2 is related to growth of an organism (may be effected by competition). It is also found that lower value of p_2 initiates higher growth rate (as shown in figure 1). Therefore p_2 could be treated as a measure of energy consumed by an organism and/or intra-specific competition. It is expected that higher degree of intra-specific competition would lower energy consumed by organism, that in turn lowers the energy allocated for growth.

3.2 Gompertzian Growth

Figure 6 represents different types of Gompertz type growth described by $\frac{ds}{dt} = -(p_1s + p_2s^2)$ with $p_2 \rightarrow 0$. It shows dependence of growth feature on p_1 . It is found that optimum growth rate [39] increases with the decrease in p_1 . But it does not alter optimum size and x_{max} .

Different types of mathematical computation models are used to study growth features of tumours [40]. In vitro and experimental studies show that the growth of tumour follows Gompertz law of growth [33] and attains a saturation level. The Gompertz law of growth ($p_2 \rightarrow 0$) indicates that the consumed energy in tumour is entirely used for reproduction ($p_1 \neq 0$). The condition $p_2 \rightarrow 0$ indicates that the intra-specific competition is negligible. In other word, the degree of cooperativity, a measure of self-organization, is very high. It is in accordance with the research work of Molski *et al.* [41]. The self-organization is also related to coherent state of the system. such coherency is confirmed by Gompertzian regression rate of tumour [41] that is found in case of external perturbations [42]. Therefore, it can be concluded that the parameter p_1 may related to the reproduction process of the system.

3.3 West-type and Von Bertalanffy type Growth

Both, West-type and von Bertalanffy type growth, are used to describe growth of organisms. According to proposed framework, the condition $\frac{ds}{dt} = -(p_1s + p_2s^2)$ with $p_2 = 0.25$ represents West-type ontogenetic growth. The variation of p_1 for West-type growth is shown in figure 4. It is found that optimum growth rate and x_{max} decrease with the increase in p_1 . The same is true in case of von Bertalanffy type growth that is described by $\frac{ds}{dt} = -(p_1s + p_2s^2)$ with $p_2 = 0.34$ (as shown in figure 5). A graphical comparison between von Bertalanffy type growth and West type biological growth is considered in figure 5 for same p_1 . It is found that specific growth rate and optimum growth rate for von Bertalanffy type growth are greater than that of West-type growth in case of same p_1 . But optimum mass and x_{max} of von Bertalanffy are lower than that of West type growth for same p_1 .

In case of West type or von Bertalanffy type growth, p_1 and p_2 are not equal to zero. The value of p_2 in case West type growth is lower than that of von Bertalanffy type growth. Therefore, it may be concluded that the ability of energy consumption is greater for West type growth than that for von Bertalanffy type growth. The lower value of growth rate for the same value

of state variable (x) for West type growth may be due to higher value of metabolic cost of survival. The nonzero value of p_1 in both cases may be an indicative of allocation of energy for reproduction from the beginning. The non-zero value of p_1 and p_2 indicates a coexistence of cooperation and competition mechanism along with reproduction in the cellular level of a growing organism.

3.4 Exponential Growth

Exponential growth is observed in different cases; e.g; autocatalytic system, radioactive decay etc. The specific growth rate is a constant quantity in these cases. Therefore, the rate of specific growth rate is zero. It means that R is equal to zero. It is also observed in case bacterial cloning [1]. It is expected that the process involved in case of bacterial cloning would be different from the processes such as autocatalytic processes. The condition $p_1 = -p_2s_0$ (as mentioned in section 2.1) shows that exponential growth may be observed for the rate equation of the specific growth rate given by,

$$\frac{ds}{dt} = -R = p_2s_0s - p_2s^2 \quad (20)$$

Therefore, it is possible to form a rate equation of specific growth rate, in case of exponential growth. It can be concluded that there are two different possibilities for which exponential growth may be observed in a growing system. In first case, rate of change of specific growth rate is zero. The rate of specific growth rate takes a functional form in the second case. The physical interpretation of it may be considered in the following way: Each term of right hand side of equation (4) may be responsible for different types of growth mechanism found in organisms with different degree of intensity. They may act independently or jointly. The collective response of two different growth mechanism [according to equation (20)] may lead to exponential growth. This finding leaves the scope to judge the exponential growth from two different point of view. It may be helpful to a researcher for better understanding of the growth mechanism of system showing exponential growth. In figure 1, the characteristic line, second from the top, represents characteristic feature of exponential growth. It shows the variation of growth rate with respect to the state variable x with the condition $p_1 = -10p_2$ (for $s_0 = 10$ and $x_0 = 0.05$).

The exponential growth observed in case of bacterial cloning [1] could be

explained in the framework of proposed first principle approach. The condition $p_1 = -p_2 s_0$ indicates a typical correlation between the energy allocation for reproduction and competition that would in term influence energy consumption. Such condition of a growing system leads to exponential. The interpretation of exponential growth of a biological system in terms of reproduction and competition is not most probably reported before. This is one of the important finding, according to the opinion of authors, reported in this communication.

3.5 Logistic and θ -logistic Growth

Figure 2 shows the variation in growth rate with state variable x for different values of p_1 in case of usual logistic growth ($p_2 = -1$). It shows that growth rate does not depends on p_1 at the initial stage of growth. But the rate of change of growth rate with respect to state variable x changes with p_1 . It increases with the decrease in p_1 . As a result, the saturated value (x_{max}) of the state variable x (for which $\frac{dx}{dt} = 0$) decreases with the increase in p_1 . It is also found that optimum growth rate and optimum size [39] increase with the decrease in p_1 .

In this proposed description of growth processes, θ - logistic growth could be addressed with the condition $p_2 < 0$. The condition $p_2 = -1$ leads to usual logistic growth. The effect of variation of p_2 on growth rate is represented by figure 3. All of the characteristic curves are logistic by nature. Among them, second from the top stands for usual logistic growth. It is found that the growth rate at the early stage, optimum growth rate, optimum size [39] and x_{max} are affected by p_2 . The value of x_{max} decreases for the condition $-1 \leq p_2 < 0$. It increases for the condition $p_2 < -1$. The initial growth rate and optimum growth rate increase with the increase in p_2 . Such dependence on p_2 can be interpreted in the following way: p_2 can be treated as a measure of intra-specific competition. If $p_2 < -1$ then the intra-specific competition is very high. As a result, the system takes more time to reach saturation level. It in turn lowers optimum growth rate. If $-1 < p_2 < 0$, then the competition is lower. Therefore, higher value of optimum growth rate and x_{max} are expected. If $p_2 = -1$ then the competition is moderate. It is also found in this study that higher value of x_{max} may be observed even in case of higher intra-specific competition than that for a moderate competition. It is not normally expected. This is one of the important findings of the proposed analysis. This finding may be helpful for the researchers

for better understanding of the effect of competitive environment on growth mechanism.

4 Conclusions

The purpose of this communication is to present a first principle approach that could capture different well-known growth models. We have identified that several types of growth models could be derived from the same rate equation of specific growth rate for different conditions. The effect of variation of different relevant parameters on growth rate and size of a physical quantity of interest have been studied in detail. It is also observed that intra-specific competition may enhance the saturated value of the state variable in some cases. We have also shown that exponential growth could be addressed from the same rate equation of specific growth rate. It is well-known fact that rate of specific growth rate is zero for exponential growth. Therefore, we identified and reported based on first principle approach, most probably for the first time, a rate equation of specific growth rate for exponential growth. It might be helpful to understand the growth mechanism of a system showing exponential growth. Therefore, the key observations are: increase in size of population in a competitive environment; and formation of rate equation of specific growth rate in case of exponential growth.

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