

A new growth curve model for biological growth: Some inferential studies on the growth of *Cirrhinus mrigala*



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ABSTRACT

Growth of living organisms is a fundamental biological process. It depicts the physiological development of the species related to the environment. Mathematical development of growth curve models has a long history since its birth. We propose a mathematical model to describe the evolution of relative growth rate as a function of time based on a real life experiment on a major Indian Carp *Cirrhinus mrigala*. We establish that the proposed model is able to describe the fish growth dynamics more accurately for our experimental data than some existing models e.g. logistic, Gompertz, exponential. Approximate expressions of the points of inflection and the time of achieving the maximum relative growth rate are derived. We study, in detail, the existence of a nonlinear least squares estimator of the model parameters and their consistency properties. Test-statistics is developed to study the equality of points of inflection and equality of the amount of time necessary to achieve the maximum relative growth rate for a species at two different locations. Using the theory of variance stabilizing transformations, we propose a new test statistic to test the effect of the decay parameter for the proposed growth law. The testing procedure is found to be more sensitive in comparison with the test based on nonlinear least squares estimates. Our proposed model provides a general framework to model growth in other disciplines as well.

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1. Introduction

Mathematical models of growth and compartmental models have been developed over a long period of time. Many growth models are introduced to model the growth of different characteristics of biological populations [1–4]. With the progress of time the main emphasis shifted from the development of a family of growth curves (describing the trend or average behavior of the population) to objective ways of fitting these models on real datasets coming from a variety of disciplines such as population ecology [5], plant biology [6], population dynamics [7], demography [8], bacterial growth [9], and behavioral ecology [10]. Recently there have been more emphasis on the problems involved in using asymptotic results to make inference from finite samples and on finding more realistic ways to model the stochastic behavior of the data as the assumption needed for a commonly used estimation method of nonlinear least squares (thereafter, NLS) are often untenable. Broadly we may distinguish two classes of mathematical models, namely, the deterministic (involving differential/partial differential equations) and the stochastic (involving probability models).

The deterministic models explore the relationship between the cause and the effect often modeled by differential equations that can be solved in a closed form where the equations are linear in nature. Nonlinear differential equations generally require some iterative algorithm. To study the uncertainty involved in the set of variables, probability assumptions are used to build the model. For example, when we deal with cells in a culture medium, the time of division of an individual cell is unknown within the mentioned limits.

In general, growth curves following a trend relationship $y = f(x; \theta)$ are fitted by NLS procedure to a given set of data, possibly after transforming the relationship to stabilize the variance. This is appropriate under the usual nonlinear regression model set up

$$y_i = f(x_i; \theta) + \epsilon_i, \quad i = 1, 2, \dots, n \quad (1)$$

where ϵ_i 's are i.i.d with mean zero and variance σ^2 . Simply adding a random or measurement error to the trend relationship is often called the 'deterministic' approach.

2. Literature survey and motivation

The literature on growth curve models is plentiful. Zotin [11] made a sincere effort on putting the known growth equations in

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chronological order that adequately describes the growth behavior of animals and plants. He suggested that three irreducible groups of equations can be distinguished from the whole suite of growth equations.

The first group (Pütter–Bertalanffy) includes the variations on the most popular (especially in hydrobiology) Bertalanffy [12,13] equation. The well known Richards' [14] formula is widely applied to plant growth [15,16]; the Gompertz function is often used to study the growth of mammals, birds [17], and tumors [18,19]. The two growth equations fall into the first group. The Gompertz equation can be obtained from both the Bertalanffy and the Richards equations [20]. Brody [21] exponential growth expression and Schmalhausen's equation of parabolic growth also fall into the first group of growth formulae [22,23].

The second group consists of those expressions of growth models in which the limiting value is expressed not by a maximal weight, but by the time when the maximal weight is achieved. The equations proposed by Zotina and Zotin [24,25] are the members of the second group. These growth formulae adequately describe the growth of fishes and some invertebrates and plants [26].

Finally the third group of growth expressions is related to the Robertson equation [27] that includes the Verhulst and logistic function [28] and also the Naydenov function [27]. Tsoularis and Wallace [1] proposed a more general family of growth curve models which incorporates most of the standard reported growth models as special cases and we call it as a T–W model. The problem of the T–W model is that there does not exist any analytical solution of X_t as a function of t . Thus fitting these types of model to real life data is a difficult job. The authors provide some approximate method for this purpose. The above family of growth curve models is described by the differential equation

$$\frac{dX_t}{dt} = b X_t^a \left[1 - \left(\frac{X_t}{c} \right)^d \right]^e \quad (2)$$

The monotonicity of relative growth rate (RGR) depends upon the choices of the parameters a , b , c , d and e . The approximate point of inflection is given by

$$t_{\text{inf}} = \frac{1}{bc^{a-1}} \left[\frac{(1 + \frac{de}{a})^{a-1/d}}{1-a} + e \frac{(1 + \frac{de}{a})^{a-1-d/d}}{1-a+d} + \frac{e(e+1)}{2!} \frac{(1 + \frac{de}{a})^{a-1-2d/d}}{1-a+2d} + \dots \right] - \frac{1}{b} \left[\frac{X_0^{1-a}}{1-a} + e \frac{X_0^{1-a+d}}{c^d(1-a+d)} + \frac{e(e+1)}{2!} \frac{X_0^{1-a+2d}}{c^{2d}(1-a+2d)} + \dots \right], \quad a \neq 1 \quad (3)$$

The simplest organisms begin to grow by the binary splitting of cells. With t denoting time and X_t the size, this leads to an exponential growth form (Malthus) $X_t = X_0 e^{bt}$ and for $b > 0$ growth is unlimited. X_0 is interpreted as the initial size. The growth response is characterized by a constant RGR and therefore has no point of inflection. The linear growth law is the simplest form of growth law which has the form, $X_t = \bar{X}bt + X_0$, $b > 0$ where \bar{X} is average size between two consecutive time points. Here the relative growth rate is an increasing function of time. This is useful to describe the growth in the early development period of fish. The time power model which does not increase as fast as exponential, is also sometimes useful in modeling biological growth. In this case RGR is a decreasing function of time, $X_t = X_0(1 + at)^b$, $a, b > 0$. The Gompertz model, based upon a model given by Gompertz in 1825 for the hazards in a life table [29], is used by many researchers across disciplines. Its initial formulation was largely empirical, but later Meadwar [30] derived it as a growth model for the heart growth of chicken. It is still one of the most widely used curves in growth mathematics. It is denoted by $X_t = X_0 e^{\frac{b}{c}(1 - \exp(-ct))}$, where $b, c > 0$.

Here the relative growth rate is an exponentially decreasing function of time. The curve has one point of inflection at $\frac{b}{c}$. The logistic equation was derived empirically by Verhulst in 1838 to describe the growth in the size of a population or organ. However, the equation also describes the rate of consumption of a monomolecular chemical substance as it breaks in an autocatalytic reaction. It is defined by $X_t = \frac{a}{1 + \exp(b(c-t))}$, where $a, b, c > 0$ (after re-parametrization). The logistic curve has one point of inflection at $t = -\frac{b}{c}$. This equation is generalized by Nelder [31] and defined generalized logistic law as $X_t = a \left(1 + X_0 e^{\left(-\frac{bt}{c} \right)} \right)^{-d}$. For both the laws, RGR is a decreasing function of time. It is a modified version of Richards [14] family of growth models described by the differential equation $\frac{dX_t}{dt} = \frac{b}{1-m} X_t \left[\left(\frac{X_t}{a} \right)^{m-1} - 1 \right]$. The Richards model includes the monomolecular model ($m = 0$), the von Bertalanffy model ($m = 2/3$), the logistic model ($m = 2$), and (by taking the limit as $m \rightarrow 1$) the Gompertz model.

The rest of the manuscript is organized in the following scheme. We propose a new growth curve model and study its mathematical properties viz., monotonicity, points of inflection, maximum relative growth rate. Gompertz law and exponential law can be derived from the proposed law. The nature of the growth curve of the other special cases is also studied. The development of this growth model is motivated by an experiment on the growth of fish *Cirrhinus mrigala*. Prior to going into the modeling aspect and statistical calibration of the proposed model, we describe the experimental protocol in detail.

3. A real life experiment

A real life experiment in an experimental pond in Indian Statistical Institute, Kolkata was performed by Fish Farm of Kalyani, West Bengal, India. The pond contained a population of hundred fishes with same age and about same size (counting from the hatching period). They were reared in the same experimental conditions before they are put into the hoopnets (hapa) in the pond. We have considered the fish *C. mrigala* for our study, which is a well studied Indian carp [32,33]. *C. mrigala* is also cultured in composite carp culture systems that include three Indian major carps as well as two Chinese carps – silver carp (*Hypophthalmichthys molitrix*) and grass carp (*Ctenopharyngodon idella*) – and common carp (*Cyprinus carpio*) [34]. In the pond there were two other common fresh water fishes, *Labeo rohita* and *Catla Catla*. The data was collected on *C. mrigala* as it has more adaptability power than the other two fishes to adjust to a new environment [35]. With the help of “multichannel analyzer” carrying in an experimental boat reading of the water quality parameters (varying throughout the year) were recorded. With an accurate metal scale, the size (longitudinal length) of the fish for each of the hoopnets was recorded. The weight of fish and some parameters on the water quality were also recorded, but they are not used in this study. Sixteen hoopnets were placed under a circular layout scheme (Fig. 1) in the pond where the fishes were confined within the net and not allowed to move anywhere in the pond.

In the circular layout model there were four directions. In each direction, four hoopnets were placed. In each net the length or size of the fish were recorded for twelve consecutive time points with a constant interval of times, i.e. once in a week (four times in a month). No food was provided to the fishes from any external sources and were allowed to grow in natural environment. We can treat these fishes confined within the four hoopnets in each direction as four different populations.

The “natural tip length” is the length between the tip of the snout (or of the lower jaw when the mouth is closed, whichever

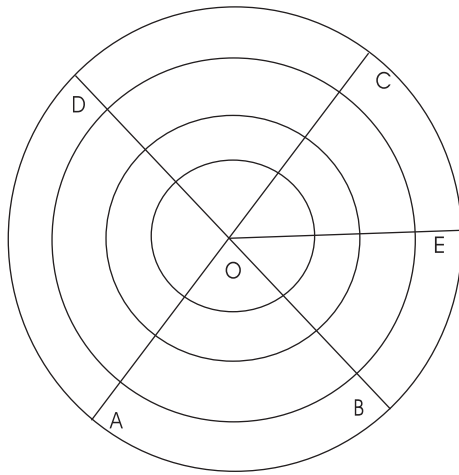


Fig. 1. Circular layout model: OA, OB, OC, OD are the four different directions. Intersection points of four concentric circles with the lines OA, OB, OC and OD are the positions of the hoopnets.

protrude further; near anterior end) and the tip of the longest lobe of the tail when held in a natural position; near the posterior end. The measurement was taken by laying the fish on a board with a movable cross hair above it, attached to an indicator running along a scale. Some other commonly used length measures are standard length, median length or fork length, total length or extreme tip length and posterior-hypural length.

In each of the experimental time points we had taken the size measurement of five replicate of fish avoiding the repeated measurements on the same individual. We put some identification mark on each of the five replicate so that they do not appear in the next drawing. In this way the cross sectional data was collected. To study the preliminary growth behavior of fish within and between directions we have plotted the size measurements of fish against different time points. It is very difficult to identify the dissimilarity between the nature of the growth process from the graphs. Rather to plot size against time point t , it would be more significant to plot empirical estimates of RGR against time point t . We want to study whether the RGR patterns along the four directions (each observed for 12 time points) are similar or not. The detail statistical analysis of the effect of water quality parameters on the growth and other aspects are studied in detail in Bhattacharya [36].

4. The model

In general fish takes some time to adapt the new ecological environment after it is put in the hoopnets. As a consequence RGR increases to achieve a maximum and then gradually decrease. But there may be some parameters that can influence the general biological and the genetical law of adaptability. So in some cases RGR may be strictly decreasing function of time due to that influence. So a general growth law is needed that can explain both the two growth processes simultaneously. In this context one can use the above generalized T–W model that can incorporate both the above cases simultaneously. It is known that for T–W model the analytical solution does not exist and one of the vital theoretical estimates i.e. the point of infection is approximate but not exact.

To overcome the drawback it is better to use a more simpler model for which the analytical solution exists and point of inflection can be computed. The Gompertz curve has been used widely in previous studies on fish growth. So we modify the Gompertz law in preference to other growth laws for our problem. The

Gompertz and the exponential model can be derived as special cases of our proposed law. For point of inflection, we have tackled the problem in a slightly different way. Rather to study the point of inflection of the growth curve we have studied the points of inflection of the RGR curve for our proposed law and that serves the purpose to identify the pattern of change of RGR with time. The model can be used to compute the time when the adaptation process accelerates to adapt the new environment. In our proposed model Eq. (4) exact expression of the points of inflection of RGR curve can be derived. Apart from this we have also evaluated the theoretical point of inflection of the growth curve approximately. The most important point to fit the proposed model Eq. (4) (as defined below), by using the empirical estimates of the RGR, is that the least square estimators always exist and satisfy the asymptotic optimum property viz. consistency, asymptotic normality, etc. We also developed test statistics to test the equality of points of inflection in two directions for Circular Layout model.

We define the differential equation of our proposed growth model is

$$\frac{1}{X_t} \frac{dX_t}{dt} = be^{-at}t^c \quad (4)$$

which has solution

$$X_t = \text{Const.} \exp \left[\int be^{-at}t^c dt \right] \quad (5)$$

It is to be noted that model (4) is a time covariate model; in a sense that, it describes the RGR as a function of time, not as a function of size. Such growth models serve the purpose of many practical applications. For example, in demography, time covariate models are used to determine the schedules of age specific fertility rates of different countries [37]. Some of the important applications of such models include: (1) measurement of the performance of an animal or group of animals with respect to time [38]; (2) study of growth comparison for different genotypes with respect to an expected growth behavior; (3) identify the key features of animal or plant growth responses with respect to different treatment combinations and environmental conditions; and (4) highly efficient use of such model to predict future performance where there is no data or measurements are available. The proposed model is more tractable than the size covariate model although both share the property of having different monotonic structures of RGR [39]. Gupta et al. [39] showed that time covariate model can detect the demographic phase change point at which developing country switches over towards a developed one. This phase change occurred at the time point at which RGR is maximized.

4.1. Plausible range and interpretation of different parameters for the proposed model

In the model (4) a and b are positive real numbers while c can be both positive and negative. To fit the Eq. (4) we can take c as a positive real number. But to find the analytical solution of the Eq. (5) c has to be a positive integer. So it is suggested that first fit the model (1) and choose the value of c to be the integer closest to the estimated value of c obtained from NLS. Then the analytic solution in closed form exists for the differential Eq. (4) with some pre-defined value of c determined in the above way. The model can be fitted through NLS algorithm for two unknown parameters a and b . When c is a negative integer especially -1 then the analytical solution does not exist, however, it is possible to study the statistical properties of the model. These are discussed below in detail when studying the special cases for different value of the parameter c .

The parameter b is called the overall rate parameter of the entire growth process [40]. The parameters a and c control the nature of the RGR in the entire growth process. Combining the nature of the two parameters a and c simultaneously the monotonicity of RGR is completely defined. It will be helpful to obtain an exact expression for the growth evolution when c is a positive integer, that will adequately help to follow the rest of the paper (see Appendix A). A general solution of the above differential Eq. (4) is given by

$$X_t = X_0 \exp \left[b c! \left(\frac{1}{a^{c+1}} - \sum_{r=0}^c \frac{t^{c-r} e^{-at}}{(c-r)! a^{r+1}} \right) \right] \quad (6)$$

where X_0 is the initial size, and $a, b \geq 0$ and c is some positive integer.

For $c = -1$ the growth function is not defined at $t = 0$. To avoid this, without loss of generality, we may take the initial time point as t_0 . Because it is always possible to transform the time axis in such a way that initial time points is $t_0 \neq 0$. Although the analytical solution does not exist in the above growth curve when $c = -1$ but we can fit the real life data by the following way:

1. First fit the model $R_t = be^{-at}t^{-1} + \epsilon_t$ by using the empirical estimates of R_t that is $\ln \left(\frac{X_{t+\Delta t}}{X_t} \right)$, by using the method of NLS estimation, where, ϵ_t 's are i.i.d. $N(0, \sigma^2)$ random variables.
2. Compute the estimate of size by the relation $\hat{X}_1 = X_0 \exp(\hat{b}e^{-at_0}t_0^{-1})$, $\hat{X}_2 = \hat{X}_1 \exp(\hat{b}e^{-at_1}t_1^{-1})$ and so on where X_0 is the initial condition which is the initial size of the cohort.

When $c = 1$ and $c = 2$, the growth curves for the proposed model are depicted separately in Fig. 2(a) and (b) respectively. For $c = -1$ the solution is depicted in (Fig. 3). RGR curves against different time intervals are drawn for different choice of parameters for our proposed growth curve model in Figs. 4 and 5 for each of the choices of c i.e. $c = 1$ and $c = 2$ respectively. The RGR curves for $c = -1$ are drawn in Fig. 6(a) and (b) (see Table 1). We list some elementary properties of the proposed model written as a function of relative growth rate.

1. X_t is monotonic increasing function of time t (see Appendix A for proof).

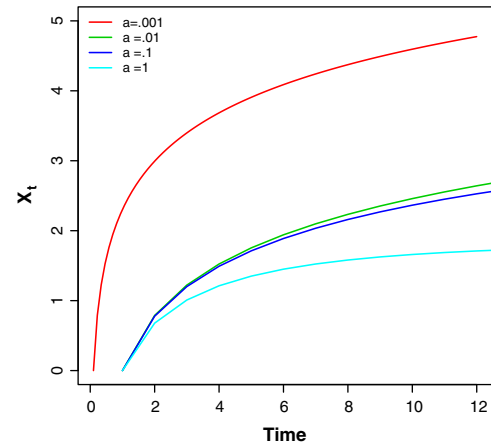


Fig. 3. Figure showing the nature of growth curve against different time points for the proposed law with $c = -1$ and $b = 1$.

2. RGR is maximum at time point $t = \frac{c}{a}$.
3. The points of inflection of the RGR curve are given by $\frac{c \pm \sqrt{c}}{a}$ which exist for $c \geq 0$.

4.2. The points of inflections of the proposed growth curve

Eq. 4 implies that

$$\frac{dX_t}{dt} = X_t b e^{-at} t^c \quad (7)$$

which implies, $\frac{d^2 X_t}{dt^2} = X_t (be^{-at} t^{c-1})(be^{-at} t^{2c-1} + c - at)$. Putting $\frac{d^2 X_t}{dt^2} = 0$, we have $b(1-at)t^{2c-1} + c - at = 0$, approximately if a is small. Similarly, for $c = 1$ and $c = 2$ this equation becomes $b(1-at)t + 1 - at = 0$ and $b(1-at)t^3 + 2 - at = 0$ respectively. For $c = 1$ the solution is $t = \frac{1}{a}$. For $c = 2$ we need to solve the four degree polynomial $bat^4 + bt^3 + at - 2 = 0$. By using Descartes' rule of sign we can conclude that the above equation has at most one positive and one negative real root and the rest of the roots are imaginary.

Point of inflection determines the size or the time at which the absolute growth rate is maximum [41] and it depicts the main difference between sigmoid growth curve models and plays an

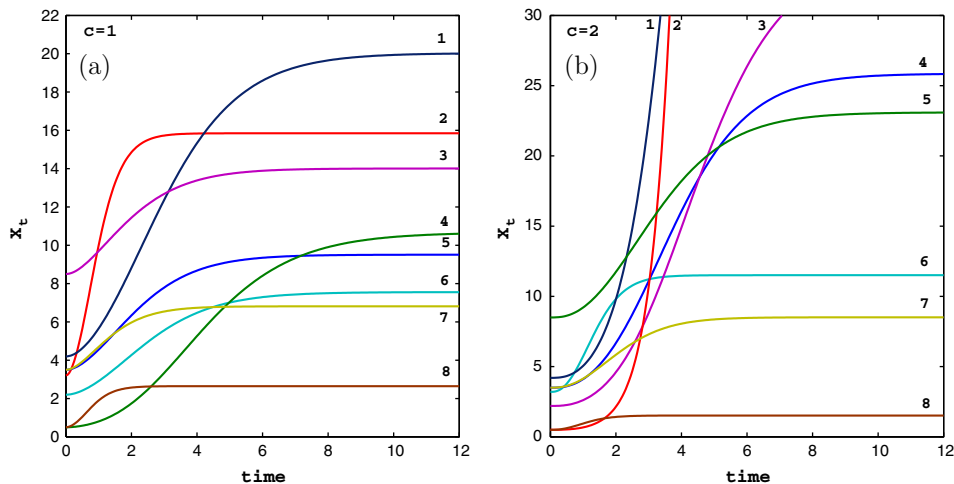


Fig. 2. (a) Evaluation of population size for the proposed modified Gompertz law for the different parameter values and $c = 1$. (1) $X_0 = 4.2$, $b = 1$, $a = 0.8$; (2) $X_0 = 0.5$, $b = 15$, $a = 3.0$; (3) $X_0 = 3.2$, $b = 10$, $a = 2.5$; (4) $X_0 = 8.5$, $b = 0.5$, $a = 1$; (5) $X_0 = 0.5$, $b = 1.5$, $a = 0.7$; (6) $X_0 = 3.5$, $b = 1$, $a = 1$; (7) $X_0 = 2.2$, $b = 1$, $a = 0.9$; (8) $X_0 = 4.0$, $b = 1.5$, $a = 1.5$. (b) Evaluation of population size for the proposed modified Gompertz law for the different parameter values and $c = 2$. (1) $X_0 = 4.2$, $b = 1$, $a = 0.8$; (2) $X_0 = 0.5$, $b = 15$, $a = 3.0$; (3) $X_0 = 3.2$, $b = 10$, $a = 2.5$; (4) $X_0 = 8.5$, $b = 0.5$, $a = 1$; (5) $X_0 = 0.5$, $b = 1.5$, $a = 0.7$; (6) $X_0 = 3.5$, $b = 1$, $a = 1$; (7) $X_0 = 2.2$, $b = 1$, $a = 0.9$; (8) $X_0 = 4.0$, $b = 1.5$, $a = 1.5$.

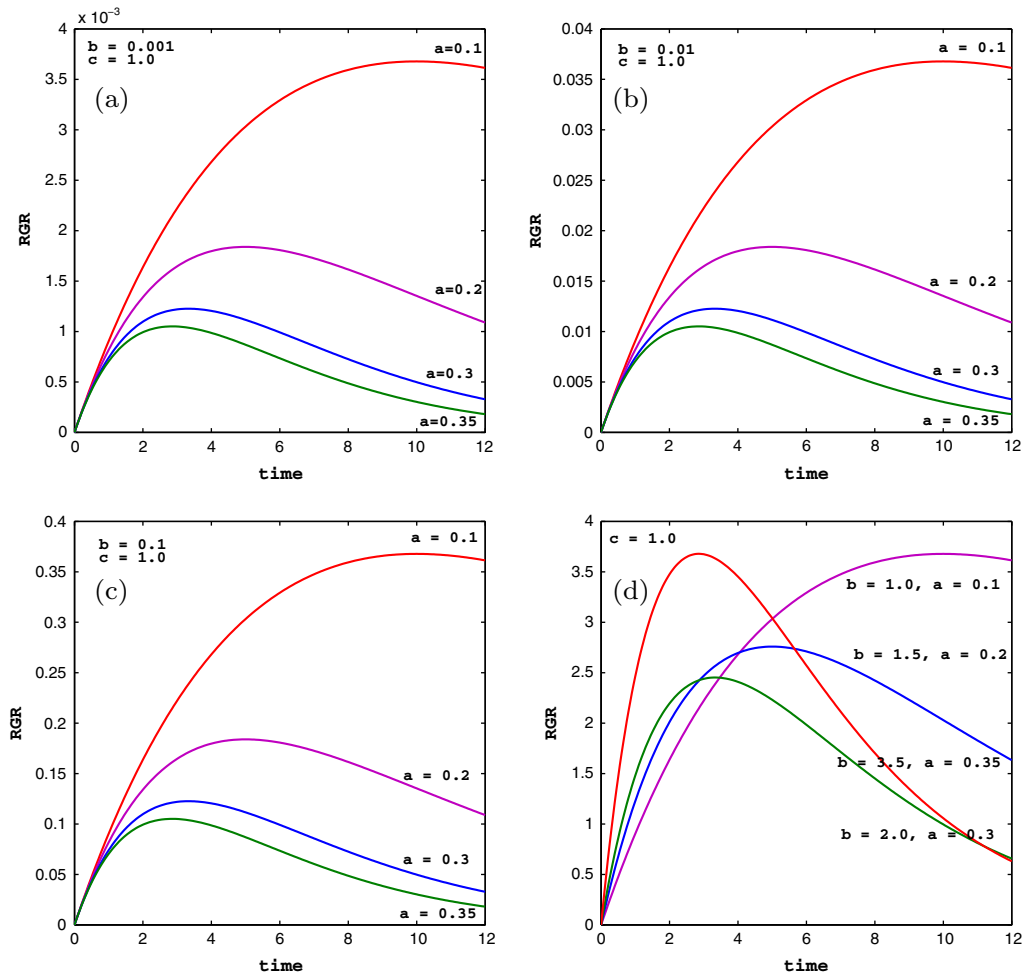


Fig. 4. Figure showing the nature of RGR against different time intervals for $c = 1$.

important role in growth curve studies across disciplines. In Richards model an additional parameter is incorporated to model the point of inflection, hence provide more flexibility in modeling exercise. This model also generally fits to plant data well and widely used in plant ecology and forestry. In growth studies of plants, estimating the inflection point as free parameter is useful as inflection point also depends on plant density [42,43].

5. Estimation of parameters

In some of the earlier problems [44] assumed the independence between the observed measurements but did not provide strong support for such assumption. While fitting growth curve models to real data, the problem can be formulated in two ways viz. (a) modeling RGR as the response variable and (b) modeling absolute growth rate as the response variable.

1. For this let us consider the models described by the stochastic differential equation

$$\frac{1}{X_t} \frac{dX_t}{dt} = \frac{d \ln X_t}{dt} = h(t; \theta) + \sigma(t; \eta) \epsilon(t) \quad (8)$$

where $\epsilon(t)$ is a stationary “Gaussian process” with $\text{var}(\epsilon(t)) = 1$ and $\sigma(t; \eta)$ is included to allow the variance of the errors changing over time (heteroscedastic). Two possible cases may arise:

- Delta Correlated Process: The error process $\epsilon(t)$ is called delta correlated if $\text{cov}(\epsilon(t_i), \epsilon(t_j)) = 0$ for all $t_i \neq t_j$. That is $\epsilon(t)$ follows i.i.d $N(0, \sigma^2)$ if $\sigma(t; \eta) = \sigma^2$ (homoscedastic). Then $y_t = \frac{1}{X_t} \frac{dX_t}{dt}$ follows independently $N(h(t; \theta), \sigma^2)$. Parameter estimate can be obtained by ordinary NLS technique and available in many statistical software packages (Matlab, R).
- Auto Correlated Process: The process is called auto correlated if $\epsilon(t)$ has stationary auto correlation function i.e., $\text{corr}(\epsilon(t_i), \epsilon(t_j)) = \rho(|t_i - t_j|)$. Then the problem is not a simple nonlinear regression problem even if we do not allow the heteroscedasticity in the process.

2. Alternatively, one could use

$$\frac{dX_t}{dt} = h(t, X_t; \theta) + \sigma(t, X_t; \eta) \epsilon(t) \quad (9)$$

But the RGR model (8) which is more useful in practice [41], fits into the framework of Eq. (9) if we take the logarithm of the size variable (i.e., use $\log y$ instead of y) and take $h(t; \theta)$ is the theoretical RGR written as a function of time t . The apparent advantage of using of RGR modeling and its applications are elaborately explained by several other authors [5,45,46]. In addition to that, generally errors in RGR modeling approximately have constant variance than the errors in absolute growth rate modeling [39,47,48]. In population prediction problems, rate modeling may often be more powerful than the usual size modeling [49]. Sometimes it is not easy, and even misleading, for the experimenter to identify the proper underlying model by studying the shape of the growth profile curves

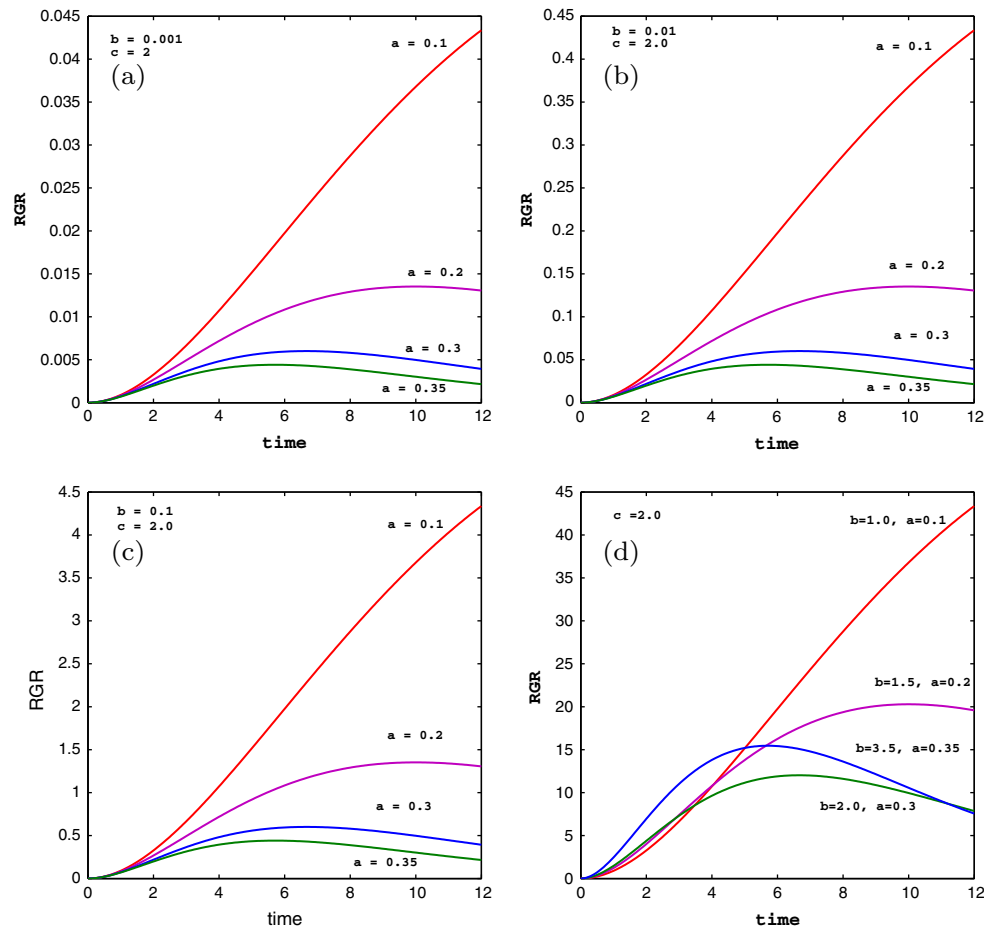


Fig. 5. Figure showing the nature of RGR against different time intervals for $c = 2$.

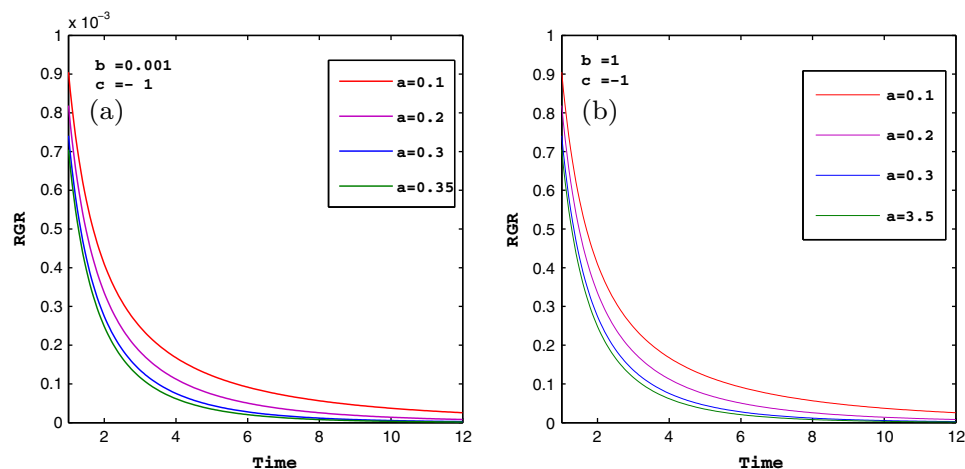


Fig. 6. Figure showing the nature of RGR against different time intervals for the proposed law when $c = -1$.

among the plenty of available growth curves. But, in comparison, if we plot the empirical estimate of RGR against time or size we can at least guess and identify the proper family of growth curves that are appropriate for the given data based on the monotonic structure of RGR. So identification of proper model is comparatively easy from RGR profile than the size profile curves. This is particularly important when growth profile curves look similar to common and existing growth curves but the RGR are not monotonically decreasing with time (Gompertz), size (logistic, Richards,

von-Bertalanffy, etc.), or constant (exponential) which are usually expected [39].

5.1. Testing of hypothesis

When fishes are transferred to the new environment, they may or may not be able cope with the environmental conditions. In the second case, RGR decays rapidly (for example, c being negative in Eq. (4) for direction C). For a fixed value of c , a is the only

parameter that determines the growth process. For example, in Fig. 6 for different values of b RGR curves are almost identical. In this case, NLS estimator is always available (explained later) but may not be suitable to test the effect of a on the growth profile when a is very small in magnitude. We propose a testing procedure to check the effect of the parameter a based on the theory of variance stabilizing transformation and is shown to have better performance than NLS method by means of simulation. This is because of the fact that, variance stabilizing transformation does not only stabilize the variance, but also normalizing at the same time.

For $c = -1$, the decay parameter a determines the nature of the RGR curve (see Fig. 3) as the rate of decay is characterized by the parameter a alone. A very small value a may not be identified through the asymptotic test based on the NLS estimate of a . We provide a new test statistic to test the hypothesis, $H_0 : a = 0$, which is more sensitive than the test based on NLS.

For $c > -1$, it is not possible to get a compact expression for the function $g(a)$ (having constant variance) using the variance stabilizing transformation. The testing procedure is recommended when $c = -1$. We have developed a new testing procedure, assuming the normality in RGR, to test $H_0 : a = 0$ against $H_1 : a > 0$ for $c \neq -1$ which is advantageous than the NLS method. Two desirable aspects of the proposed test are: (1) it does not involve the estimated value of the other parameters in the expression of variance of the decay parameter, so exact asymptotic expression for the estimated variance can be derived and (2) the test can be used to identify the intervals where the growth process does not follow the underlying growth law, that is, an interval specific test for the parameters can be developed. This new testing procedure is based on the work by Bhattacharya et al. [45] and Bhowmick et al. [40]. We will not present the results in the manuscript but some related results are depicted in Appendix C.

5.2. Test of significance of a for $c = -1$

Let $y_t = \frac{1}{x_t} \frac{dx_t}{dt}$ and $f(t, \theta) = be^{-at}t^{-1}$; with $e_t \sim N(0, \sigma^2)$ for $t = 1, \dots, n$ and $y_t \sim N(be^{-at}t^{-1}, \sigma^2)$ the equation

$$y_t = f(t, \theta) + e_t \quad (10)$$

defines a regression model. The model parameters a , b can be estimated using the NLS method by minimizing the error sum of squares $S^2 = \sum_{t=1}^n e_t^2 = \sum_{t=1}^n (y_t - be^{-at}t^{-1})^2$ with respect to a and b . These NLS estimates are also the maximum likelihood estimates (MLE) under the normality assumption of errors [41]. So we can treat these estimates as MLE also.

In many experimental situations biologists may have some prior knowledge about the value of the parameter b , the overall rate parameter of the entire growth process. Even if when it is not known, b can be treated as the average of RGR for all the time intervals in the whole experimental time frame and carry out the significant test of a for the model (10) after fitting through NLS. For the inferential aspect of the parameter a , we let that $b = b_0$ be known. Let,

$$\begin{aligned} F(a) &= (b_0 e^{-a} 1^{-1}, b_0 e^{-a2} 2^{-1}, \dots, b_0 e^{-an} n^{-1})' \\ F'(a) &= \left(\left(\frac{\partial f_i(t)}{\partial \theta_j} \right) \right)_{i=1, \dots, n} \\ &= \left(\frac{\partial(b_0 e^{-a} 1^{-1})}{\partial a}, \frac{\partial(b_0 e^{-a2} 2^{-1})}{\partial a}, \dots, \frac{\partial(b_0 e^{-an} n^{-1})}{\partial a} \right)' \\ &= (b_0 e^{-a} 1^{-1}(-1), b_0 e^{-a2} 2^{-1}(-2), \dots, b_0 e^{-an} n^{-1}(-n))' \\ [F'(a)]' F(a) &= \sum_{t=1}^n b_0^2 e^{-2at} \end{aligned}$$

From the theory of nonlinear regression we have, $\hat{a} \sim N(a, \sigma^2(F'F)^{-1})$ where $\text{var}(\hat{a}) = \frac{\sigma^2}{b_0^2 \sum_{t=1}^n e^{-2at}}$ [41]. Let us consider a transformation $g(a)$ of a such that the variance of the transformation is constant i.e. $\left[\frac{dg(a)}{da} \right]^2 \frac{\sigma^2}{b_0^2 \sum_{t=1}^n e^{-2at}} = c^2 = \text{var}(g(\hat{a}))$. Integrating both sides, we have after simplification

$$g(a) = \left[2\sqrt{m} + \sum_{j=1}^{n-1} \frac{m^{j+1/2}}{2j+1} \right] \quad (11)$$

where $m = e^{-2a}$. We can take any arbitrary value for c . So let, $c^2 = \frac{4a^2}{b_0^2}$, so that $\text{var}[g(\hat{a})] = \frac{4a^2}{b_0^2}$ implying $g(\hat{a}) \sim N(g(a), \frac{4a^2}{b_0^2})$. The distribution of $\tau_2 = \frac{g(\hat{a}) - g(a)}{\frac{2a}{b_0}}$ converges more rapidly to $N(0, 1)$ compared to $\tau_1 = \frac{\hat{a} - a}{\frac{\sigma^2}{b_0^2 \sum_{t=1}^n e^{-2at}}}$, which follows from the theory of variance stabilizing transformation (see Fig. 7). The derivation of the transformation $g(a)$ is given in B. Rewriting $g(a)$ in terms of a using $m = e^{-2a}$ we have, $g(a) = \left[2\sqrt{\frac{1}{e^{2a}}} + \sum_{j=1}^{n-1} \frac{e^{-a(2j+1)}}{2j+1} \right]$, so that

$$g(\hat{a}) = \left[2\sqrt{\frac{1}{e^{2\hat{a}}}} + \sum_{j=1}^{n-1} \frac{e^{-\hat{a}(2j+1)}}{2j+1} \right] \quad (12)$$

We now consider following hypothesis testing problem for the decay parameter a ,

$$H_0 : a = 0 \quad \text{against} \quad H_1 : a \neq 0 \quad (13)$$

at the α level of significance based on the measurement data $\{y_t\}_1^n$ generated following the nonlinear regression model Eq. (10) with t as input variable. The test statistic τ_1 is used to test the hypothesis. It is better to test

$$H_0 : g(a) = 2 + \sum_{j=1}^{n-1} \left(\frac{1}{2j+1} \right) \quad \text{against}$$

$$H_1 : g(a) \neq 2 + \sum_{j=1}^{n-1} \left(\frac{1}{2j+1} \right) \quad (14)$$

by using the test statistic τ_2 , because the convergence to normality of τ_2 is faster than the test statistic τ_1 (Fig. 8). To compare the performance of the test we have simulated 1000 datasets of length 20 for different values of a from the interval (0.001, 0.5) using the following set of parameter values, $b = 1$, $c = -1$ and the independent variable $t = 1, 2, \dots, 20$. The simulation is performed using the model (10), where $e_t \sim N(0, \sigma^2)$. We fix the value of σ as 0.1. For each dataset, we run nonlinear regression procedure (using “nls” function in R [50]) and record the corresponding p -values for the test $H_0 : a = 0$. Using our proposed test we compute the p -values for $H_0 : g(a) = 2 + \sum_{j=1}^{n-1} \left(\frac{1}{2j+1} \right)$. Both the set of p -values are plotted against the values of a . In Fig. 8 the red and blue dots denote p -values corresponding to the tests $H_0 : a = 0$ and $H_0 : g(a) = 2 + \sum_{j=1}^{n-1} \left(\frac{1}{2j+1} \right)$ respectively. It is to be noted that, for large values of a ($> .1$) our proposed test reject the null hypothesis with better accuracy (lower p -value, < 0.001 in almost all cases) whereas the usual test rejects the null hypothesis only for about 13% of the cases. For lower values of a , our proposed test is more sensitive as it rejects the null hypothesis (about 74% times) even for very low but positive values of a , whereas the usual test accepts the null hypothesis about 80% times with p -value being greater than 0.05. Thus, our proposed test is more sensitive in making inference about the decay parameter. It is able to detect very small effect of the decay parameter in the growth process. In some biological processes, it may appear that, the rate of a growth process is decaying over time with a very small decay rate. In such a case, to identify the true underlying

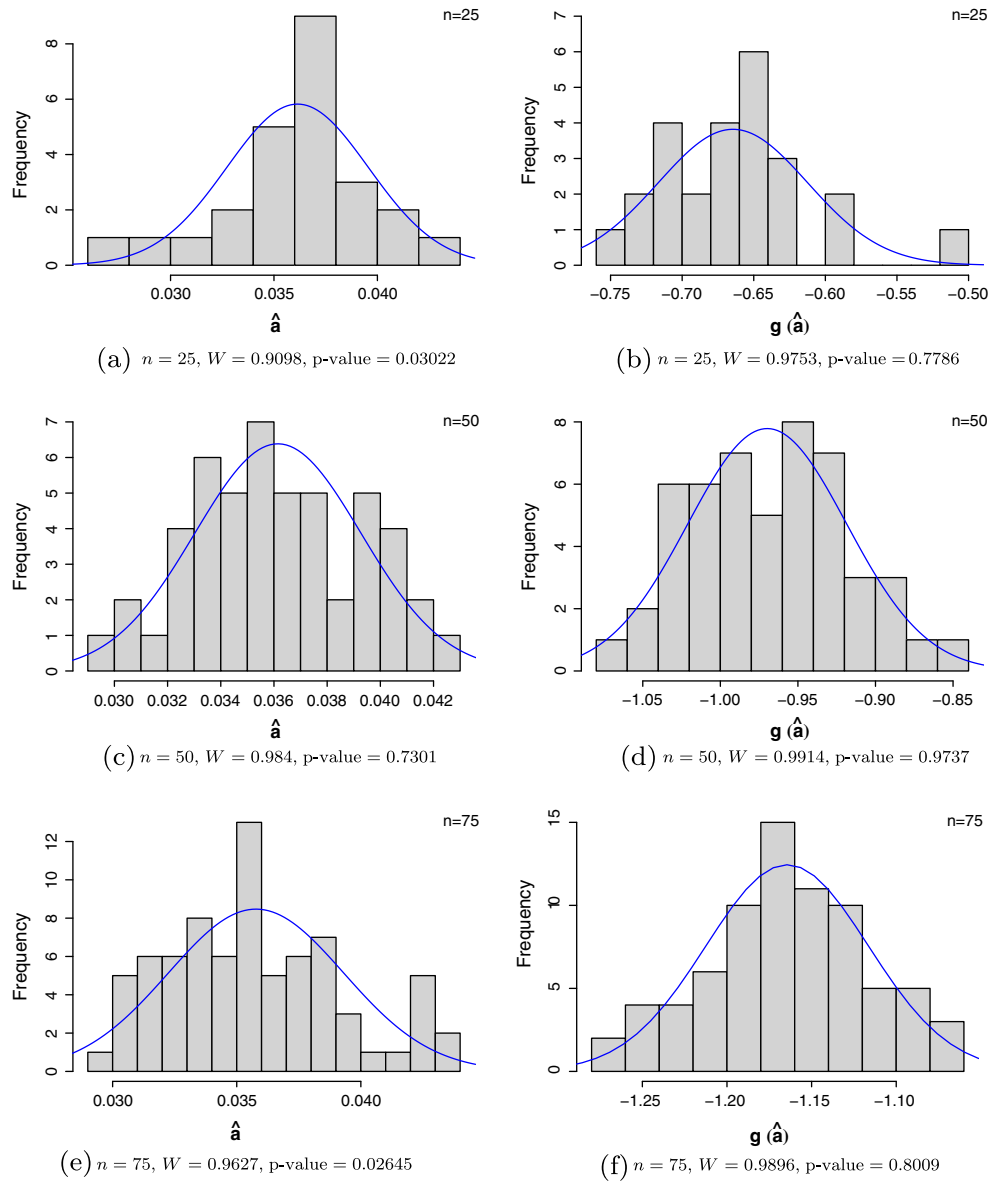


Fig. 7. The left panel represents the histogram of estimated \hat{a} and the right panel represents the histogram of $g(\hat{a})$. We tested that, if the sample size increases do the distributions of \hat{a} and $g(\hat{a})$ converge to normality? (a) For $n = 25$, 100 sample of size n is generated using $a = 0.036$, $b = 1$ and $\sigma = 0.01$. For each dataset, we obtained \hat{a} using NLS and density histogram is plotted using these 100 values of \hat{a} . Densities based on empirical data is overlayed on the histogram. Shapiro-Wilk test is performed to check the normality in the distribution of \hat{a} . A p -value < 0.05 denotes the rejection of the null hypothesis that, the distribution is normal. The other figures (c) and (e) are generated in the same way. For all 100 samples $g(\hat{a})$ is also calculated and its density histograms are plotted in (b), (d) and (f). Note that, in left panel, as n increases, the convergence in normality is not guaranteed. The Shapiro-Wilk test rejects the asymptotic normality of the distribution of \hat{a} for $n = 25$ and $n = 75$, whereas accepts for $n = 50$. The distribution of $g(\hat{a})$ is more consistent with increasing sample size and converges to normality more rapidly.

process, the proposed test would be more appropriate. It also demonstrates that, the proposed test is sensitive to the choice of the decay parameter in a sense that, it can give correct decision when a is small. The procedure was carried out with different choices of $b(0.1, 0.5, 1.5, 2)$ and $\sigma(0.01, 0.05)$ and the overall conclusion of the test was verified.

5.3. Existence of NLS estimator of the proposed model

Let us consider fitting of the model (4) to real data. By using the empirical estimate of RGR as $R_t = \frac{1}{\Delta t} \log \left(\frac{X_{t+\Delta t}}{X_t} \right)$, we can approximate the left hand side of Eq. (4). After using this empirical estimates, the Eq. (4) becomes

$$R_t = be^{-at}t^c + \epsilon_t \quad (15)$$

and $\hat{\theta}$ is chosen to be the NLS estimator of the parameter θ if it minimizes the following function

$$S_n(\theta) = \sum_t [R_t - be^{-at}t^c]^2 = \sum_t [R_t - f(\theta, t)]^2 \quad (16)$$

where $\theta = (b, a, c)'$. In case of Eq. (15) we make the following assumptions:

1. ϵ_t 's are independently normally distributed with mean zero and variance σ^2 ($\sigma^2 > 0$).
2. Now for each nonzero t , $f(\theta, t)$ is a continuous function of θ defined on Θ . Without loss of generality we can take t as nonzero because if it is zero then the time axis can be transformed in such a way so that it is nonzero.
3. Θ is closed, bounded (i.e. compact) subset of \mathfrak{R}^3 .

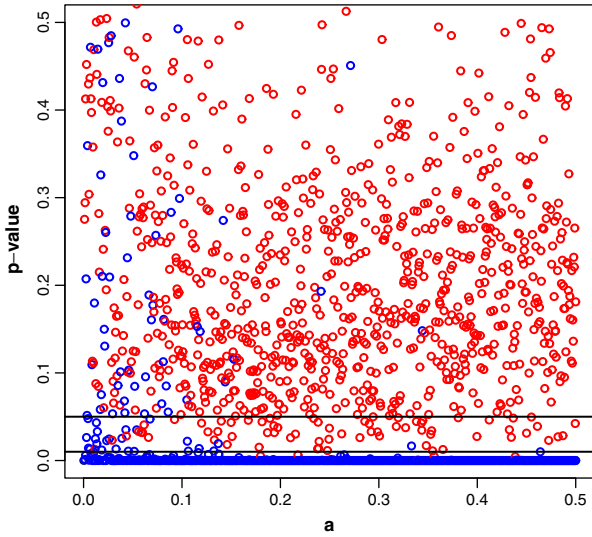


Fig. 8. The interval (0.001, 0.5) is divided in 1000 subintervals. For each value of a a dataset of length 20 is generated with $b = 1$, $c = -1$, $\sigma = 0.1$ using model Eq. (10) (see text). Model (10) is fitted to each of the 1000 datasets. The red dots represent the p -value corresponding to the test $H_0: a = 0$ and the blue dots represent the p -value corresponding to the test $H_0: g(a) = 2 + \sum_{j=1}^{n-1} \left(\frac{1}{2^j+1}\right)$. The horizontal lines represent 5% and 1% cut off for the p -value. The proposed test (blue dots) is more likely to reject the null hypothesis at large values of a than the usual test based on NLS. The proposed test also performs better at small but positive values of a (of order 10^{-2}) as it can detect a very low rate of decay exhibited by the growth process. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Following Jennrich [51] it can be shown that the NLS estimator exists for the parameters of the nonlinear regression model (15). The boundedness of Θ as described above is not a serious restriction, as most parameters are bounded by the physical constraints of the system being modeled. In the model (4) $a \in [a_0, M_1]$ & $b \in [b_0, M_2]$, where a_0, b_0, M_1, M_2 are some positive numbers. c can take both positive and negative value as per as RGR is “first increasing then decreasing” or “strictly decreasing” function of time. c is assumed to take values interval $[-m_3, M_3]$, where m_3, M_3 are positive numbers.

5.4. Consistency of the NLS estimators of the model parameters

The sketch of the proof mainly follows from the work of Jennrich [51], Malinvaud [52] and Wu [53] (see also, Gallant [54]). Let θ^{**} be the true value of the parameter vector θ . To prove the consistency of the NLS estimator $\hat{\theta}$ the first step is to show that θ^{**} uniquely minimizes $\text{plim } S_n(\theta)$, where $\text{plim } T_n(\theta) = \beta$ implies $T_n \xrightarrow{p} \beta$ (convergence in probability). If n is sufficiently large so that $n^{-1}S_n(\theta)$ is close to $\text{plim } S_n(\theta)$, then $\hat{\theta}$ which minimizes the former, will be close to θ^{**} , which minimizes the latter. This gives the weak consistency. Now considering the Eq. (15), we have

$$\begin{aligned} n^{-1}S_n(\theta) &= n^{-1} \sum_t [R_t - f(\theta, t)]^2 \\ &= n^{-1} \sum_t [R_t - f(\theta^{**}, t) + f(\theta^{**}, t) - f(\theta, t)]^2 \\ &= n^{-1} \sum_t [\epsilon_t + f(\theta^{**}, t) - f(\theta, t)]^2 \\ &= n^{-1} \sum_t \epsilon_t^2 + 2n^{-1} \sum_t \epsilon_t [f(\theta^{**}, t) - f(\theta, t)] + n^{-1} \sum_t [f(\theta^{**}, t) - f(\theta, t)]^2 \\ &= C_1 + C_2 + C_3 \text{ (say)} \end{aligned}$$

By law of large numbers, $\text{plim } C_1 = \sigma^2$. For fixed θ^{**} and θ , $\text{plim } C_2$ follows from the convergence of $\left\{n^{-1} \sum_t [f(\theta^{**}, t) - f(\theta, t)]^2\right\}$. By Chebychev's inequality:

$$\begin{aligned} P\left(n^{-1} \sum_t \epsilon_t [f(\theta^{**}, t) - f(\theta, t)] > \epsilon\right) \\ < \frac{\sigma^2}{\epsilon^2 n^2} \sum_t [f(\theta^{**}, t) - f(\theta, t)]^2 \end{aligned} \quad (17)$$

Since the uniform convergence of C_2 follows from the uniform convergence of the right-hand side of the inequality (17), it suffices to assume that, $\frac{1}{n} \sum_t f(\theta_1, t) f(\theta_2, t)$ converges uniformly in $\theta_1, \theta_2 \in \Theta$. Hence $\text{plim } S_n(\theta)$ will have a unique minimum at θ^{**} if $\lim_{n \rightarrow \infty} C_3$ has a unique minimum at θ^{**} which will follow the weak consistency. Define,

$$B_n(\theta_1, \theta_2) = \sum_t f(\theta_1, t) f(\theta_2, t) \quad (18)$$

$$D_n(\theta_1, \theta_2) = \sum_t [f(\theta_1, t) - f(\theta_2, t)]^2 \quad (19)$$

In addition to the previous three assumptions we make the following two more assumptions:

- $n^{-1}B_n(\theta_1, \theta_2)$ converges uniformly for all θ_1, θ_2 in Θ to function $B(\theta_1, \theta_2)$. This implies, by expanding Eq. (19), that $n^{-1}D_n(\theta_1, \theta_2)$ converges uniformly to $D(\theta_1, \theta_2) = B(\theta_1, \theta_1) + B(\theta_2, \theta_2) - 2B(\theta_1, \theta_2)$.
- $D(\theta, \theta^{**}) = 0$ if and only if $\theta = \theta^{**}$.

For our proposed model

$$\begin{aligned} B_n(\theta_1, \theta_2) &= \sum_t f(\theta_1, t) f(\theta_2, t) = \sum_t b_1 b_2 e^{-(a_1+a_2)t} t^{c_1+c_2} \\ &= b_1 b_2 \sum_t e^{-(a_1+a_2)t} t^{c_1+c_2} = k \sum_{t=1}^n m^t t^p, \text{ say} \end{aligned} \quad (20)$$

where $m = e^{-(a_1+a_2)} < 1$, $p = c_1 + c_2$ and $k = b_1 b_2$. Convergence of the above series (20) $\{u_n\}$ (say) is guaranteed by using ratio test. The ratio of $(n+1)$ th and n th terms is defined by $\frac{u_{n+1}}{u_n} = \frac{m^{n+1}(n+1)^p}{m^n n^p}$. This implies $\lim_{n \rightarrow \infty} \frac{u_{n+1}}{u_n} = m < 1$ showing that the series is convergent provided $a \in (a_0, M_1]$. This implies that, $B_n(\theta_1, \theta_2)$ converges uniformly to $B(\theta_1, \theta_2)$. So the least square estimator of the parameter θ for our proposed growth curve model is consistent.

5.5. Inference and data analysis

Suppose in the two directions the theoretical solution of the time points at which the maximum RGR is attained are t_0 and t_1 , (say) where t_0 and t_1 are defined as $\frac{c_0}{a_0}$ and $\frac{c_1}{a_1}$, respectively. (a_0, c_0) and (a_1, c_1) are the parameters of the growth curve for the first and second directions respectively. We can test whether the theoretical solution of the time points at which the maximum RGR value is observed, are same or different along two specific directions. We write the null and alternative hypothesis as

$$H_{10}: \frac{c_0}{a_0} = \frac{c_1}{a_1} \quad \text{against} \quad H_{11}: \frac{c_0}{a_0} \neq \frac{c_1}{a_1}$$

From asymptotic properties of MLE we can say that, $\hat{\theta}_i \sim N(\theta_i, \text{var}(\hat{\theta}_i))$, for $i = 1, 2, 3$ and $\hat{t}_k \sim N(t_k, \text{var}(\hat{t}_k))$, for $k = 0, 1$ where $\hat{\theta} = (\hat{a}, \hat{b}, \hat{c}) = (\hat{\theta}_1, \hat{\theta}_2, \hat{\theta}_3)$. Let us define the MLE of (a_0, c_0, a_1, c_1) as $(\hat{a}_0, \hat{c}_0, \hat{a}_1, \hat{c}_1)$. By the invariance property of maximum likelihood estimator [55]: since t_0 and t_1 are functions of the parameters (a_0, c_0, a_1, c_1) so the MLE of t_0 and t_1 are \hat{t}_0, \hat{t}_1 respectively, where $\hat{t}_0 = \frac{\hat{a}_0}{\hat{c}_0}$ and $\hat{t}_1 = \frac{\hat{a}_1}{\hat{c}_1}$. The variances of the above estimators and the covariances between the two estimators are the asymptotic variances and covariances respectively. Similarly, like above we can also draw inference on the theoretical points of inflection of

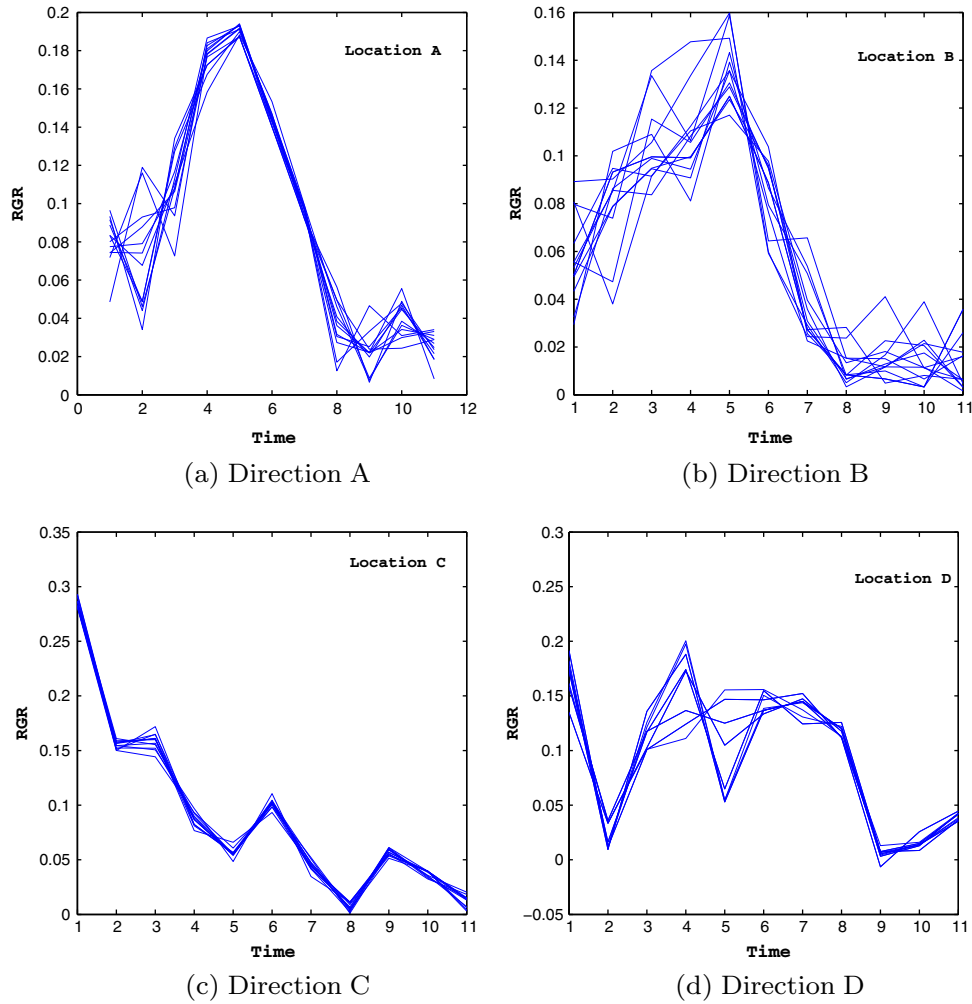


Fig. 9. Combined graph of RGR for all 12 samples against the time intervals.

Table 1
Special cases of Model (4) for different parameter values.

Parameter values	The differential Eq. (4) $\left(\frac{1}{X_t} \frac{dX_t}{dt}\right)$	Growth model
$c = 0$	be^{-at}	$X_t = X_0 e^{\frac{b}{a}(1 - \exp(-at))}$
$a = 0, c = 0$	b	$X_t = X_0 e^{bt}$
$c = 1$	$be^{-at}t$	$X_t = X_0 e^{\frac{b}{a}(1 - \exp(-at)(t + \frac{1}{a}))}$
$c = 2$	$be^{-at}t^2$	$X_t = X_0 e^{\frac{b}{a^2}(1 - \exp(-at)(t^2 + 2t + \frac{2}{a^2}))}$
$c = -1$	$be^{-at}t^{-1}$	$X_t = \text{Const.} \exp[bt^{-1}e^{-at}dt]$

the RGR curves, $t_{0\text{inf}}$ and $t_{1\text{inf}}$ between two growth models, where, $t_{0\text{inf}} = \frac{c_0 + \sqrt{c_0}}{a_0}$ and $t_{1\text{inf}} = \frac{c_1 + \sqrt{c_1}}{a_1}$. Using the usual notation,

$$H_{20} : \frac{c_0 + \sqrt{c_0}}{a_0} = \frac{c_1 + \sqrt{c_1}}{a_1} \quad \text{against} \quad H_{21} : \frac{c_0 + \sqrt{c_0}}{a_0} \neq \frac{c_1 + \sqrt{c_1}}{a_1}$$

or

$$H_{20} : \frac{c_0 - \sqrt{c_0}}{a_0} = \frac{c_1 - \sqrt{c_1}}{a_1} \quad \text{against} \quad H_{21} : \frac{c_0 - \sqrt{c_0}}{a_0} \neq \frac{c_1 - \sqrt{c_1}}{a_1}$$

Table 2
Parameter estimates and RSS of proposed and various growth laws for direction A.

Model	\hat{b}	Pr ($> t $)	SE (\hat{b})	\hat{a}	Pr ($> t $)	SE (\hat{a})	R-square	AIC ^c	RMSE
Model (4) ($c = 2$)	0.07961	0.003097	0.01989	0.5281	1.929e-06	0.04905	0.6736	-39.7	0.1005
Model (4) ($c = 1$)	0.1161	0.004757	0.0312	0.3102	0.0002054	0.0518	0.4235	-35.19	0.1234
Exponential	0.09016	0.0005331	0.01801	—	—	—	—	-27.82	0.1889
Gompertz ^a	0.1404	0.0144	0.04645	0.07695	0.2401	0.06118	0.1585	-28.35	0.1684
Power	1.55	0.3692	1.64	0.09048	0.5194	0.135	0.09739	-27.74	0.1731
Logistic ^b	0.1868	0.01266	0.06019	0.3613	0.02598	0.1358	0.227	-29.39	0.1606

^a In the estimation procedure, RGR is expressed as function of time. For power law, $\text{RGR} = b \log\left(1 + \frac{a}{1+at}\right)$.

^b For the logistic growth, $\text{RGR} = \frac{be^{-bt}(a-X_0)}{X_0 + e^{-bt}(a-X_0)}$, where X_0 is the initial mean weight of the fish population under study.

^c AIC is obtained using AIC function in R from the “nls” routine in R Development Core Team [50].

Table 3
Parameter estimates and RSS of proposed and various growth laws for direction B.

Model	\hat{b}	Pr ($> t $)	SE (\hat{b})	\hat{a}	Pr ($> t $)	SE (\hat{a})	R-square	AIC	RMSE
Model (4) ($c = 2$)	0.08171	0.001028	0.01716	0.6164	3.975e−07	0.04755	0.798	−50.92	0.06037
Model (4) ($c = 1$)	0.1058	0.001879	0.02438	0.3717	4.672e−05	0.05106	0.6102	−45.58	0.07694
Exponential	0.05991	0.00133	0.01361	–	–	–	–	−33.99	0.1427
Gompertz	0.116	0.009336	0.03524	0.1174	0.1005	0.06415	0.3023	−37.09	0.1132
Power	0.7094	0.223	0.542	0.1713	0.4461	0.215	0.1845	−35.72	0.1205
Logistic	0.1939	0.01184	0.06166	0.1374	0.0009537	0.02853	0.3643	−38.13	0.108

Table 4
Parameter estimates and RSS of proposed and various growth laws for direction C.

Model	\hat{b}	Pr ($> t $)	SE (\hat{b})	\hat{a}	Pr ($> t $)	SE (\hat{a})	R-square	AIC	RMSE
Model (4) ($c = -1$)	0.292	5.862e−06	0.031	−0.03156	0.3897	0.03492	0.8922	−43.08	0.08622
Model (4) ($c = -0.5$)	0.3192	3.13e−06	0.03141	0.1235	0.005415	0.03394	0.9174	−46.31	0.07444
Gompertz	0.116	0.009336	0.03524	0.1174	0.1005	0.06415	0.3023	−37.09	0.1132
Power	0.7094	0.223	0.542	0.1713	0.4461	0.215	0.1845	−35.72	0.1205
Logistic	0.1939	0.01184	0.06166	0.1374	0.0009537	0.02853	0.3643	−38.13	0.108

Table 5
Parameter estimates and RSS of proposed and various growth laws for direction D.

Model	\hat{b}	Pr ($> t $)	SE (\hat{b})	\hat{a}	Pr ($> t $)	SE (\hat{a})	R-square	AIC	RMSE
Model (4) ($c = 2$)	0.06107	0.07279	0.03007	0.4868	0.0004337	0.09017	0.3136	−26.61	0.1823
Model (4) ($c = 1$)	0.1066	0.032	0.04206	0.2979	0.002985	0.07397	0.2347	−27.59	0.1744
Exponential	0.09305	0.0005858	0.01883	–	–	–	–	−26.85	0.1975
Gompertz	0.1499	0.01428	0.04948	0.08403	0.2116	0.06249	0.1791	−27.43	0.1756
Power	1.292	0.2831	1.132	0.1253	0.4714	0.1667	0.1407	−27.05	0.1787
Logistic	0.1886	0.01497	0.06287	0.3872	0.03323	0.1542	0.2115	−27.98	0.1713

5.6. The test statistics

The test statistics for the above two tests are respectively,

$$\tau_1 = \frac{(\hat{t}_0 - \hat{t}_1) - (t_0 - t_1)}{\sqrt{\text{var}(\hat{t}_0) + \text{var}(\hat{t}_1)}}$$

$$\tau_2 = \frac{(\hat{t}_{0\text{inf}} - \hat{t}_{1\text{inf}}) - (t_0 - t_1)}{\sqrt{\text{var}(\hat{t}_{0\text{inf}}) + \text{var}(\hat{t}_{1\text{inf}})}}$$

Under H_{10} or H_{20} both τ_1 and $\tau_2 \sim N(0, 1)$. So H_{10} and H_{20} are rejected at $\alpha\%$ level of significance if

$$|\tau_1| > \tau_{1,\alpha/2} \quad \text{and} \quad |\tau_2| > \tau_{2,\alpha/2}$$

To evaluate the variance terms in the test statistics let us consider the following general formula for the function of estimators

$$\begin{aligned} \text{var}(f(\hat{\gamma}, \hat{\beta})) &= \text{var}(\hat{\gamma}) \left(\frac{\partial f}{\partial \gamma} \right)^2 \Big|_{\hat{\gamma}, \hat{\beta}} + \text{var}(\hat{\beta}) \left(\frac{\partial f}{\partial \beta} \right)^2 \Big|_{\hat{\gamma}, \hat{\beta}} \\ &+ \text{cov}(\hat{\gamma}, \hat{\beta}) \left(\frac{\partial^2 f}{\partial \gamma \partial \beta} \right) \Big|_{\hat{\gamma}, \hat{\beta}} \end{aligned} \tag{21}$$

where $f(\hat{\gamma}, \hat{\beta})$ is any nonlinear function of the parameters [41] (Chapter 5). By using Eq. (21) we can calculate the variances of the estimators \hat{t}_0 , \hat{t}_1 , $\hat{t}_{0\text{inf}}$ and $\hat{t}_{1\text{inf}}$. Thus we obtain the following expression,

$$\begin{aligned} \text{var}\left(\frac{\hat{c}}{\hat{a}}\right) &= \text{var}(\hat{a}) \left(\frac{\hat{c}^2}{\hat{a}^4}\right) + \text{var}(\hat{c}) \left(\frac{1}{\hat{a}}\right)^2 + \text{cov}(\hat{a}, \hat{c}) \left(\frac{1}{\hat{a}^4}\right) \\ \text{var}\left(\frac{\hat{c} + \sqrt{\hat{c}}}{\hat{a}}\right) &= \text{var}(\hat{a}) \left(\frac{\hat{c} + \sqrt{\hat{c}}}{\hat{a}^2}\right)^2 + \text{var}(\hat{c}) \left(\frac{1 + \frac{1}{2\sqrt{\hat{c}}}}{\hat{a}}\right)^2 \\ &+ \text{cov}(\hat{a}, \hat{c}) \left(\frac{1 + \frac{1}{2\sqrt{\hat{c}}}}{\hat{a}^2}\right). \end{aligned}$$

6. Results and discussion

By simple scatter plots of empirical estimate of RGR versus time, we observed that the nature of monotonicity of RGR is almost same in directions A and B (Fig. 9(a) and (b)). In direction C the pattern is not same with directions A and B (Fig. 9(c)). In direction D the RGR pattern is irregular. This might have occurred due to the variability in water quality parameters viz. dissolved oxygen, temperature, etc. in different directions (see Fig. 9(d)).

We have fitted the proposed law to the data collected from directions A, B, C and D by choosing different values of c . We have previously described a simple rule on how to determine the value of the parameter c . By using the empirical estimate of RGR we have fitted the Eq. (4). In all the cases we used the cross sectional data of different directions. We have provided the summary of the results of fitting exercise in Tables 2–5 and the corresponding figures are depicted in Fig. 10. The fitting exercise is performed using nonlinear regression routine implemented in R package for statistical computing [50]. To compare the fitting results we have computed three commonly used measures of goodness of fit viz. coefficient of determination (R^2), Akaike information criterion (AIC) and root mean square error (RMSE).

We observe that if we increase the value of the parameter c from zero (which is the Gompertz law) to 1 and 2, we achieved better model fitting to the data from direction A and B (Tables 2 and 3). The Eq. (4) with $c = 2$ gives better fitting among the other set of models viz. model (4) with $c = 1$, exponential, Gompertz, logistic and power. In comparison with the Gompertz law, proposed model (4) fits better with respect to R^2 , AIC and RMSE. In fact only the model (4) identified the pattern of the RGR over different time points. Since our aim is to model RGR with respect to time, to compare its goodness of fit with other models, RGR is expressed on a timely basis. In direction C model (4) with $c = -0.5$ gives best fit as observed from the R^2 , AIC and RMSE values from Table 4. In direction D model (4) with $c = 2$ provides the best fit with respect

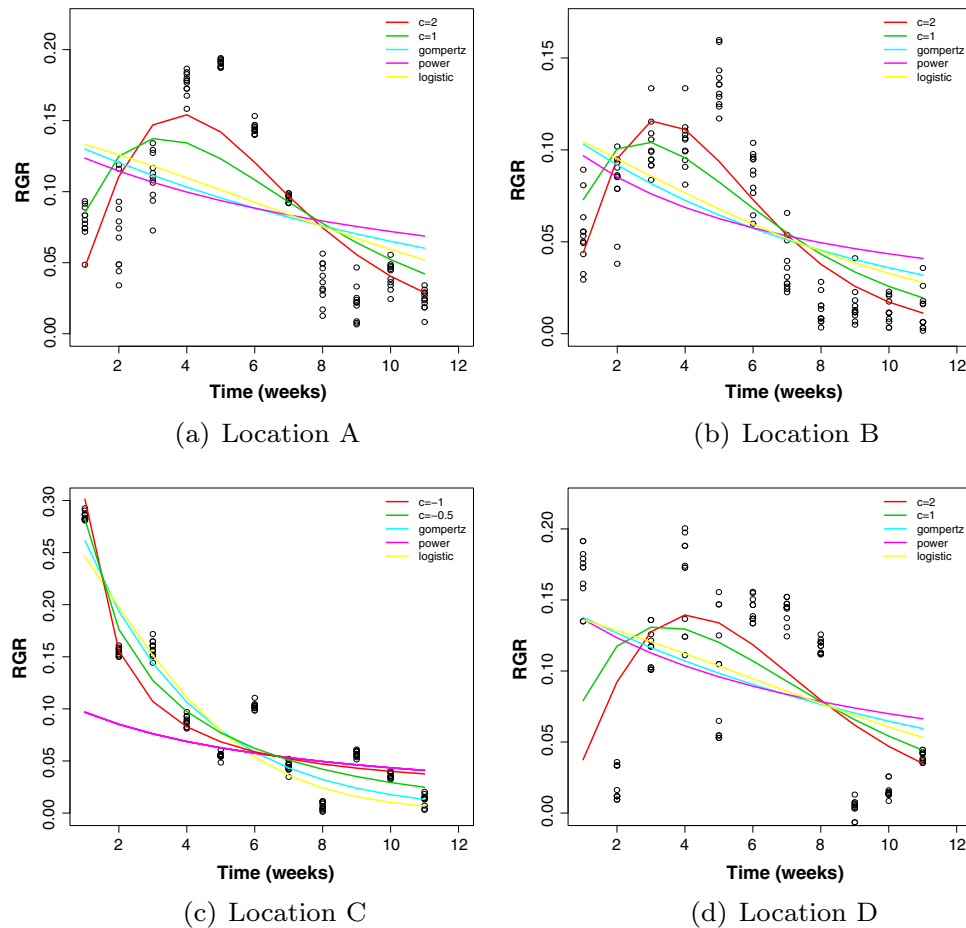


Fig. 10. Fitting of five candidate models for location A and B and their comparison is shown in Tables 2–5.

to R^2 values, but logistic growth gives the best fit while comparing the goodness of fit using AIC and RMSE (Table 5).

As already discussed, it is important to test the equality of the theoretical solution of the time points at which RGR is maximum. We test the hypothesis using a testing procedure as described in the previous section. Based on the above test we found a significant difference in mean time at which RGR is maximized in directions A and B with a p -value 0.006779022 (<0.05 and 0.01 , $\tau_{\text{obs}} = 7.183823$). In direction A, maximum RGR is attained in 4th week ($\hat{t}_0 = 4.283941$, $\text{SE} = 0.0795126$) while in direction B RGR is maximized in 3rd week ($\hat{t}_1 = 3.412673$, $\text{SE} = 0.09158088$). There is no need to carry out this type of testing for the directions C and D, because in direction C RGR is always maximized at the initial time point. In direction D, RGR varies in an irregular manner.

We also carry out the test of equality of the points of inflections of the RGR curves for the two directions A and B. There is no point of inflection of RGR curve in direction C. In direction D we can fit our proposed law but the theoretical estimate of the point of inflection may not carry much weight as RGR may have more than one mode. So we carry out the above test for the directions A and B only using our proposed test statistic. We observed that H_{20} is accepted; there is no significant difference between $t_{0\text{inf}}$ and $t_{1\text{inf}}$ at 5% level of significance ($P = 0.094$). However, the test marginally rejects the null hypothesis at 10% level of significance.

7. Conclusion

Growth of living individuals (plants/animals) is a continuous process and determining its source of variation about other

demographic or environmental covariates is of immense importance. RGR is one of the widely used metric to measure the growth rate. Therefore, a flexible family of growth model of RGR with respect to time is a major requirement to describe the growth pattern. The model described in this article serves this purpose efficiently, especially for our data on fish growth. The proposed time covariate model is simple and flexible enough to represent all types of feasible monotonic and nonmonotonic structures of RGR with respect to time. In addition, this model may provide a general framework (with other standard models as special cases) to model growth phenomena across disciplines. It may be a future endeavor to explore its applicability in other areas of growth study.

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Appendix A. Lemma 1

Lemma Appendix. 1. A general solution of the above differential equation Eq. (4) is given by

$$X_t = X_0 \exp \left[bc! \left(\frac{1}{a^{c+1}} - \sum_{r=0}^c \frac{t^{c-r} e^{-at}}{(c-r)! a^{r+1}} \right) \right]$$

where X_0 is the initial size, and $a, b \geq 0$ and c is some positive integer.

Proof. We have

$$\frac{1}{X_t} \frac{dX_t}{dt} = be^{-at} t^c$$

Integrating both sides we get

$$\int d \ln X_t = \int be^{-at} t^c dt + k, \Rightarrow \ln X_t = \int be^{-at} t^c dt + k \Rightarrow \ln X_t = bl(a, c) + k, \text{ say}$$

Now,

$$\begin{aligned} I(a, c) &= -\frac{1}{a} t^c e^{-at} + I(a, c-1) \text{ [using integration by parts]} \\ &= -\frac{1}{a} t^c e^{-at} - \frac{c}{a^2} t^{c-1} e^{-at} - \frac{c(c-1)}{a^3} I(a, c-2) \\ &= -\frac{1}{a} t^c e^{-at} - \frac{c}{a^2} t^{c-1} e^{-at} - \frac{c(c-1)}{a^3} t^{c-2} e^{-at} \\ &\quad - \dots - \frac{c(c-1) \dots 3.2.1}{a^c} I(a, 0) \\ &= -\frac{1}{a} t^c e^{-at} - \frac{c}{a^2} t^{c-1} e^{-at} - \frac{c(c-1)}{a^3} t^{c-2} e^{-at} \\ &\quad - \dots - \frac{c(c-1) \dots 3.2.1}{a^{c+1}} e^{-at} \end{aligned} \quad (\text{A.1})$$

where $I(a, 0) = e^{-at} dt = -\frac{e^{-at}}{a}$. Now from initial condition when $t = 0, k = \frac{bc(c-1) \dots 3.2.1}{a^{c+1}} + \ln X_0$. This implies

$$\begin{aligned} X_t &= X_0 \exp \left[\frac{bc(c-1) \dots 3.2.1}{a^{c+1}} - b \left[\frac{t^c}{a} + \frac{ct^{c-1}}{a^2} + \frac{c(c-1)t^{c-2}}{a^3} \dots \right. \right. \\ &\quad \left. \left. + \frac{c(c-1) \dots 3.2.1}{a^{c+1}} \right] e^{-at} \right] \\ &= X_0 \exp \left[\frac{bc(c-1) \dots 3.2.1}{a^{c+1}} - b \left[\frac{t^c}{a} + \frac{ct^{c-1}}{a^2} + \frac{c(c-1)t^{c-2}}{a^3} \dots \right. \right. \\ &\quad \left. \left. + \frac{c(c-1) \dots 3.2.1}{a^{c+1}} \right] e^{-at} \right] \quad \square \end{aligned} \quad (\text{A.2})$$

Appendix B. Computation of $g(a)$

$$\begin{aligned} \Rightarrow g(a) &= \frac{cb_0}{\sigma} \int \sqrt{\sum_{t=1}^n e^{-2at}} da \\ \Rightarrow g(a) &= \frac{cb_0}{\sigma} \int \sqrt{\sum_{t=1}^n m^t} \frac{dm}{-2m}, \text{ where } e^{-2a} = m, \Rightarrow da = \frac{dm}{-2m} \\ \Rightarrow g(a) &= \left(\frac{cb_0}{-2\sigma} \right) \int \sqrt{\sum_{t=1}^n m^t} \frac{dm}{m} \\ \Rightarrow g(a) &= \int \left[\frac{m(1-m^n)}{(1-m)} \right]^{1/2} \frac{1}{m} dm \text{ as } m < 1 \text{ (taking } c = -\frac{2\sigma}{b_0}) \\ \Rightarrow g(a) &= \int \frac{1}{\sqrt{m}} \left(\frac{1-m+m-m^n}{1-m} \right)^{1/2} dm \\ \Rightarrow g(a) &= \int \frac{1}{\sqrt{m}} \left(1 + \frac{m-m^n}{1-m} \right)^{1/2} dm \\ \Rightarrow g(a) &\simeq \int \frac{1}{\sqrt{m}} \left(1 + \frac{1}{2} \left(\frac{m-m^n}{1-m} \right) \right) dm \\ \Rightarrow g(a) &= \left[\int \frac{1}{\sqrt{m}} dm + \frac{1}{2} \int \sqrt{m} \left(\frac{1-m^{n-1}}{1-m} \right) dm \right] \\ \Rightarrow g(a) &= \left[\frac{\sqrt{m}}{1/2} + \frac{1}{2} \int \sqrt{m} (1-m^{n-1})(1+m+m^2+\dots) dm \right] \end{aligned}$$

$$\begin{aligned} \Rightarrow g(a) &= \left[2\sqrt{m} + \frac{1}{2} \int \sqrt{m} \left[\sum_{j=1}^{\infty} m^{j-1} - \sum_{j=1}^{\infty} m^{n-1+j-1} \right] dm \right] \\ \Rightarrow g(a) &= \left[2\sqrt{m} + \frac{1}{2} \int \sqrt{m} \left[\sum_{j=1}^{n-1} m^{j-1} \right] dm \right] \\ \Rightarrow g(a) &= \left[2\sqrt{m} + \frac{1}{2} \int \sum_{j=1}^{n-1} m^{j-1/2} dm \right] \\ \Rightarrow g(a) &= \left[2\sqrt{m} + \frac{1}{2} \sum_{j=1}^{n-1} \frac{m^{j+1/2}}{j+1/2} \right] \end{aligned}$$

Appendix C. An alternative estimation procedure

The proposed model is given by,

$$R(t) = be^{-at} t^c$$

Taking logarithm in both sides and then using Δ operator we have the interval specific estimate of c , given by,

$$\hat{c}_t = \frac{1}{n} \sum_{i=1}^n \frac{\Delta^2 \ln \widehat{R}_i(t)}{\Delta^2 \ln t}$$

where $\widehat{R}_i(t)$ denotes the estimate of $R(t)$ based on one sample (i th individual). Similarly, we obtain the estimate of the interval specific estimate of a , say \hat{a}_t , where

$$\hat{a}_t = \hat{c}_t \Delta t - \frac{1}{n} \sum_{i=1}^n \Delta^2 \ln \widehat{R}_i(t)$$

We have also shown that, \hat{a}_t is normally distributed with mean $\Delta^2 \ln R(t) - \Delta \ln R(t)$ and variance $V_a(t)$, which is given by the following expression,

$$V_a(t) = \left[\frac{\Delta \ln t}{\Delta^2 \ln t} \right]^2 \frac{V_{\Delta^2}(t)}{n} + \frac{V_{\Delta}(t)}{n} - 2 \frac{\Delta \ln t}{n} \text{Cov} \left[\hat{c}_t, \sum_{i=1}^n \Delta \ln \widehat{R}_i(t) \right]$$

where

$$V_{\Delta}(t) = \sigma^2 \left[\frac{1}{R^2(t+1)} + \frac{1}{R(t)} - \frac{2\rho}{R(t)R(t+1)} \right]$$

and

$$\begin{aligned} V_{\Delta^2}(t) &= \sigma^2 \left[\frac{1}{R^2(t+2)} + \frac{4}{R^2(t+1)} + \frac{1}{R^2(t)} + \frac{2\rho^2}{R(t+2)R(t)} \right. \\ &\quad \left. - \frac{4\rho}{R(t+1)} \left\{ \frac{1}{R(t)} + \frac{1}{R(t+2)} \right\} \right] \end{aligned}$$

The covariance term $\text{Cov}[\hat{c}_t, \sum_{i=1}^n \Delta \ln \widehat{R}_i(t)]$ is given by,

$$\frac{\sigma^2}{\Delta^2 \ln t} \left[\frac{\rho}{R(t+1)} \left\{ \frac{1}{R(t)} + \frac{1}{R(t+2)} \right\} - \left\{ \frac{1}{R^2(t+1)} + \frac{\rho^2}{R(t)R(t+2)} \right\} - \frac{V_{\Delta}(t)}{\sigma^2} \right]$$

ρ represents the correlation between $\ln \widehat{R}_i(t)$ and $\ln \widehat{R}_i(t+1)$. In addition to that, \hat{a}_t is a consistent estimator of a_t . Then computing the covariance between \hat{a}_t and \widehat{a}_{t+s} we developed a testing procedure for testing the significance of the parameter a . This testing procedure has two fold implications: (1) It gives us an idea about the effect of the parameters in certain intervals of overall growth phase and (2) These effects in aggregation endow us with an overall goodness of fit of the model in the whole growth phase.

Lemma Appendix. 2. X_t is monotonic increasing function of time t .

Proof. To show that X_t is a monotonic increasing function of t it is sufficient to prove $f(t) = \int b e^{(-at)} t^c dt$ is a monotonic increasing function of t . Since $b > 0$, for any $t_1 > t_2 > 0$, $f(t_2) - f(t_1) = \int_{t_1}^{t_2} b e^{(-at)} t^c dt > 0$, which is always true as the above definite integral is the area under the curve $b e^{(-at)} t^c$ for the interval (t_1, t_2) so it is always positive. That implies $f(t_2) - f(t_1) > 0 \Rightarrow f(t_2) > f(t_1)$. So $X_{t_2} > X_{t_1}$ for any $t_1, t_2 > 0$, and hence the result. \square

Lemma Appendix. 3. The points of inflection of the RGR curve is given by $\frac{c \pm \sqrt{c}}{a}$.

Proof. We have $R'_t = R_t \left[\left(\frac{c}{t} - a \right)^2 - \frac{c}{t^2} \right]$

Now, $R''_t = 0 \Rightarrow t = \frac{c \pm \sqrt{c}}{a}$. So, the two points of inflections are $\frac{c + \sqrt{c}}{a}$ and $\frac{c - \sqrt{c}}{a}$. \square

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