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A unified approach to the Richards-model family for use in growth analyses: Why we need only two model forms

Even Tjørve*, Kathleen M.C. Tjørve

Lillehammer University College, Faculty of Economics and Organisation Science, P.O. Box 952, NO-2604 Lillehammer, Norway

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ABSTRACT

This paper advances a unified approach to the modeling of sigmoid organismal growth. There are numerous studies on growth, and there have been several proposals and applications of candidate models. Still, a lack of interpretation of the parameter values persists and, consequently, differences in growth patterns have riddled this field. A candidate regression model as a tool should be able to assess and compare growth-curve shapes, systematically and precisely. The Richards models constitute a useful family of growth models that amongst a multitude of parameterizations, re-parameterizations and special cases, include familiar models such as the negative exponential, the logistic, the Bertalanffy and the Gompertz. We have reviewed and systemized this family of models. We demonstrate that two specific parameterizations (or re-parameterizations) of the Richards model are able to substitute, and thus to unify all other forms and models. This *unified-Richards model* (with its two forms) constitutes a powerful tool for an interpretation of important characteristics of observed growth patterns, namely, [I] maximum (relative) growth rate (i.e., slope at inflection), [II] age at maximum growth rate (i.e., time at inflection), [III] relative mass or length at maximum growth rate (i.e., relative value at an inflection), [IV] value at age zero (i.e., birth, hatching or germination), and [V] asymptotic value (i.e., adult weight or length). These five parameters can characterize uniquely any sigmoid-growth data. To date most studies only compare what is referred to as the “growth-rate constant” or simply “growth rate” (k). This parameter can be interpreted as neither relative nor actual growth rate, but only as a parameter that affects the slope at inflection. We fitted the unified-Richards and five other candidate models to six artificial data sets, generated from the same models, and made a comparison based on the corrected Akaike's Information Criterion (AICc). The outcome may in part be the result of the random generation of data points. Still, in conclusion, the unified-Richards model performed consistently well for all data sets, despite the penalty imposed by the AICc.

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1. Introduction

Analyses of growth over time often fit a curve to a scatter plot. Different growth measurements may be studied, including body mass, body length or length of different parts of the body. The growth of plants and animals may asymptote towards adult size, although some organisms keep growing, if at slower rates, their whole lives. (Fish, for instance, do not exhibit asymptotic growth.) Growth curves of some organisms take on more complicated patterns, as in stature growth in humans, for example, where the growth rate across time produces a bimodal curve. Still, most growth curves are expected to be sigmoid and asymptotic. Typically, initial growth (close to germination, hatching or birth) is slow before increasing in speed and finally leveling off toward adult values, and a sigmoid growth curve results. The models we

discuss here (apart from the exponential model) are sigmoid with an upper asymptote.

Ratkowsky (1983, 1990) and France and Thornley (1984, 2007) have provided good reviews of useful candidate regression models (for plant and animal growth). There is, however, considerable confusion in the literature because models are frequently presented in many forms (different parameterizations and re-parameterizations), and sometimes the same model is given different names, perhaps because the author(s) simply did not recognize the model. Also, many familiar models are actually only parameterizations or generalizations of other well known ones; for instance, the Richards model is a parameterization of the negative-exponential model and a generalization both of the logistic model and of the von Bertalanffy model.

Models can often be written in different forms by which parameters take on new meanings; for example, the well known logistic model can be written as $y = a/(1 + c_1 \exp(bx))$ or as $y = a/(1 + \exp(b(x - c_2)))$, where $c_2 = \ln(c_1)/b$. Parameter c_1 affects both how sigmoid curve (i.e., slope at an inflection) is and the x -value

* Corresponding author. Tel.: +47 612 88 219; fax: +47 612 88170.
E-mail address: even.tjorve@hil.no (E. Tjørve).

at inflection. Parameter c_2 equals x at an inflection (and only affects this). Often authors are unaware of these differences or are unable to choose a model form that is suitable for their purpose, or both. The failure to recognize which models are and are not nested can also result in the application of the wrong method for comparing the fit of the two models, say, by an F -test, Akaike's Information Criterion (AIC) (Akaike, 1974) or Bayesian Information Criterion (BIC) (Schwarz, 1978).

Here, we review a particular class of models, the Richards family, which produce curves with a sigmoid shape and an upper asymptote. The models of this family are good choices for regression analyses of sigmoid growth curves. We discuss mainly different versions (re-parameterizations) of the four-parameter Richards model. These are particularly useful when the aim is to compare growth curves between groups of organisms or between different biometric measurements in a single species. Some of these allow for the fixing of both the upper asymptote and the initial (germination, birth or hatching) values. In this type of model, both the upper asymptote (adult value) and the initial value can be represented by a separate (single) parameter.

The primary aim of this paper is to determine amongst the many model forms and versions the one or the few of these that may be most suitable for discussing, characterizing, and comparing the growth of different biometric measurements and between populations or species. The corollary of this objective is the identification of superfluous models in the literature, which involves an account of the models, parameterizations, and re-parameterizations of members of the Richards family.

The above approach does not necessarily warrant elaborate testing of model performance. We will confine our model testing to limited number of artificial data sets, and test the suggested models against other candidate models or model forms.

2. The Richards family of models

In the following, we apply a notation where W is the value of the growth measurement (mass or length) at time t . The parameters most commonly found in the models discussed are: A ; upper asymptote, B ; lower asymptote or minimum, k ; the growth-rate constant (which controls the slope at an inflection, i.e., maximum slope or how sigmoid curve is), K ; maximum relative growth rate (as found at inflection), T_i ; time at an inflection, T_0 ; time at $W=0$, W_0 ; value at $t=0$, d , and δ ; exponent or part thereof (which controls the inflection value, W_i), and S ; a parameter which controls an inflection time.

2.1. The benefit of re-parameterization

Some forms (or re-parameterizations) are more useful than others, because specific curve characteristics (as starting value, placement of inflection, and maximum slope) are given by a single parameter (or a simple function of a single parameter). This is illustrated by what is perhaps the best known model, the logistic, which may be given as $A/(1+S \exp(-kt))$, but it can also be re-parameterized and presented on the form $A/(1+\exp(-k(t-T_i)))$. Here, instead of the S -parameter, it has the parameter T_i , which is time (i.e., age) at an inflection. The latter form is the more useful, because we can calculate the placement of the inflection point directly. With the logistic model, the inflection always falls at 50% of the upper asymptote. The coordinates for the inflection point, therefore, simply becomes $(T_i, A/2)$. Most models or parameterizations, we discuss here, can be presented on a form, where T_i is given as a single parameter, which is often called a location parameter, because it shifts curve horizontally without changing its shape. The forms of the logistic model above can also be

re-parameterized to read $A/(1+(A-W_0)/W_0 \exp(-kt))$, where W_0 is the initial value (mass or some length measure), i.e., the value where curve intersects with the y -axis (at $t=0$). The model with the initial value (W_0) as a separate parameter may be rewritten (re-parameterized) in several other ways (see below and Appendix A), but curve shape and other properties remain the same. In these forms, the W_0 -parameter can be substituted with an initial value (e.g. average) calculated from the population or the species, thus fixing the parameter value. Still, this is rarely performed. The logistic model has the x -axis as a lower asymptote, but some models have, always or only for certain parameter values, a starting point on the x -axis (which may in reality be a minimum, but where we ignore everything to the left of this starting point). For example, the von Bertalanffy model, when given as $A(1 - \exp(-k(t-T_0)))^3$, for example, contains the starting point on the x -axis, T_0 , as a separate parameter.

In addition to such re-parameterizations, we discuss the properties of additional parameters that change the inflection value, W_i , (and thus also curve shape) and parameters that move curve horizontally and vertically, as well as how the latter can be used to compress curve, whilst keeping the upper asymptote constant.

2.2. Common family members

Richards class or family of related models can be shown to include well known models such as the negative exponential, the logistic model (Verhulst, 1838), von Bertalanffy model (Bertalanffy, 1938), and Gompertz model (Gompertz, 1825). We show how these models are nested in the Richards model (Richards, 1959; Richards, 1969), and are thus special cases of this model. Also, other models which are suggested under different names are in fact no more than parameterizations or re-parameterizations of Richards model.

A three-parameter version of the Richards model, often called the Chapman–Richards model (Chapman, 1961; Pienaar and Turnbull, 1973; Tjørve, 2003; Tjørve, 2009) is given as $A(1 - \exp(-kt))^d$. It has its starting point at the origin of axes, which is only useful if growth begins at zero (not at a birth, hatching or germination value).

By the addition of one parameter, S , this model becomes

$$A(1 - S \exp(-kt))^d, \quad (1)$$

where S moves curve horizontally (without changing its shape). This model has a complementary form

$$A/(1 + S \exp(-kt))^d. \quad (2)$$

These represent the simplest and most compact forms of the four-parameter Richards model. Model (1) produces sigmoid shapes for $d > 1$, and has a starting point on the x -axis. Model (2) produces sigmoid shapes for $d < 0$, and has the x -axis as a lower asymptote. In the first case (model (1)), the inflection value approaches A/e when $d \rightarrow \infty$, and in the second case (model (2)) the relative value approaches A/e when $d \rightarrow (-\infty)$. This may cause iterative regression algorithms to get lost trying to calculate. Note that the ranges (for d) where the models are sigmoid will change if the sign for the d -parameter is reversed. The first form, (1), can be written as $A/(1 - S \exp(-kt))^{-d}$ and latter form as $A(1 + S \exp(-kt))^{-d}$. Model (1) can also be re-parameterized to a form, where the starting point becomes a single parameter (instead of S)

$$A(1 - \exp(-k(t-T_0)))^d, \quad (3)$$

which can also be written as $A/(1 - \exp(-k(t-T_0)))^{-d}$. Schnute (1981) referred to these models as the “Bertalanffy form,” but

presents it on a re-parameterized form given as $A(1 - \exp(-k(t - T_0)))^{1/d}$.

Richards model has a floating inflection value, which can be given as a proportion of the upper asymptote. This proportion is determined by the exponent (in the above case d or $-d$). Models (1) and (3) consequently have inflection values which will vary between 0 and A/e , whereas model (2) has an inflection value which vary between A/e and A . These two groups of forms represent complementary versions of Richards model. Each pair covers inflection points at the whole range from 0% to 100% of the upper asymptote. In our case, models (1) and (2) complement each other because the inflection value of the first is restricted between 0 and A/e , and the latter between A/e and A ; thus, covering the range 0–100%.

We now move to another type of Richards models, where only one version is needed to cover all inflection values between 0% and 100% of the upper asymptote. These should be more useful than those, where two model forms are needed to cover all inflections values. If $1/d$ is included into model (3), we have

$$A(1 - (1/d)\exp(-k(t - T_i)))^d. \quad (4)$$

In this form, no complementary version is needed, as the first minus sign changes to plus when the d goes from plus to minus. Therefore, this form is sigmoid for both $d > 1$ and $d < 0$ and has a starting point on the x -axis for the first range and a lower asymptote for the second range. The form is the same (has exactly the same shape for equal parameter values) as $A/(1 - (1/d)\exp(-k(t - T_i)))^{-d}$. If $(1/d)$ is substituted for $-d$ in this model, Richards model becomes

$$A/(1 + d\exp(-k(t - T_i)))^{1/d}. \quad (5)$$

which is sigmoid for all $d > -1$, has a starting point for $-1 < d < 0$ and has a lower asymptote for $d > 0$. Again, model (5) is the same as $A(1 + d\exp(-k(t - T_i)))^{1/-d}$.

Model (5) may be a more useful form of Richards model, when is fitted by an iterative nonlinear regression, because there is no leap in d -value, where the model changes from having a lower asymptote to having a starting point on the x -axis. This is because it (a) covers both the version with a lower asymptote and the version with a starting point (in the same model form), and (b) the inflection value changes continually with a continual change in d -value. If one prefers a form where only positive values of the d -parameter are considered, this is achieved by

$$A(1 + (d-1)\exp(-k(t - T_i)))^{1/(1-d)} \quad (6)$$

(or $A(1 - (1-d)\exp(-k(t - T_i)))^{1/(1-d)}$) which is sigmoid for $d > 0$, has a starting point for $0 < d < 1$ and has a lower asymptote for $d > 1$ (and therefore also changes continually along with a continual change in the d -value). The expression for the exponent not only changes the ranges of the d -parameter that produces sigmoid curves, but also the expression for the inflection value that is a function of d . In other words, the d -parameter alone determines the inflection value (between 0% and 100% of the upper asymptote), as shown in Fig. 1. Where the exponent is d , as in models (1)–(4), the inflection value (i.e., mass or length at the time of an inflection) becomes $A(1 - (1/d))^d$, whereas if the exponent is $1/d$, as in model (5), the inflection value becomes $A(1 - d)^{1/d}$, and if the exponent is $1/(1 - d)$, as in model (6), the inflection falls at $Ad^{1/(1-d)}$.

We have now discussed both Richards models in T_i -forms (where time of inflection is a fitted parameter) and in T_0 -forms (where instead time at zero value is a parameter). We can then move on to the W_0 -forms, where the value at time zero (W_0) is a fitted parameter (instead of T_i or T_0). If based on model (6) the W_0 -form becomes

$$A(1 + ((W_0/A)^{(1-d)} - 1)\exp(-kt))^{1/(1-d)}. \quad (7)$$

This model, (7), has the same properties (for different values of d) as model (6). In Appendix A, there are 24 re-parameterizations of this model. All 24 can also be written with $(1 - d)$ and with $1/(1 - d)$ in place of d .

The last group of Richards models that we examine is the compressed form, which comprises parameterizations, where a fifth parameter is added. This parameter, B , gives the lower asymptote. For example, model (6) then becomes

$$B + (A - B)(1 + (d-1)\exp(-k(t - T_i)))^{1/(1-d)}, \quad (8)$$

which goes from having B as a lower asymptote to having a starting point (at $W=B$). Again, if fitted as a nonlinear regression by computer, it may be safest to use this form or the form, where the exponent is $1/d$ or $1/(1 - d)$ rather than d in order to reduce the risk of non-convergence. (Typically, regression software displays a message telling the user that the model is “not converging,” if it cannot fit a useful regression curve in, for example, 1000 iterations.)

Another interesting version of model (6) is found in Sugden et al. (1981) and has been applied to growth data in several studies, such as Aggrey (2002) (domestic chickens) Aggrey et al. (2003) (quails), Frie et al. (2003) (seals), Krafft et al. (2006) (seals),

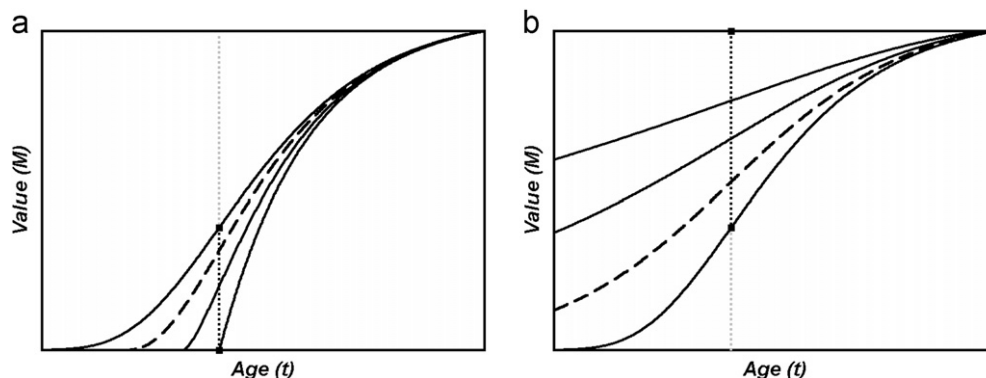


Fig. 1. Richards curves where all parameters, but the d -parameter are kept constant, constructed from model (6), $A/(1 + (d-1)\exp(-k(t - T_i)))^{1/(1-d)}$. The dotted line represents age at an inflection, T_i , so that the inflection point for each curve falls, where the dotted line intersects curve. Panel (a) shows curves for $0 < d < 1$, which have a starting point on the x -axis and inflection values between zero and A/e (i.e., 36.8% of the upper asymptote). Here, the lower curve is the negative exponential model (which represents $d=0$), and the dashed curve is the von Bertalanffy model (which represents $d=2/3$). Panel (b) shows curves for $d > 1$, which has the x -axis as lower asymptote and inflection values between A/e and the upper asymptote (A). Here, the dashed curve is the logistic model (which represents $d=1$). We note that an A/e is the inflection value, where the model goes from having a lower asymptote to having a starting point on the x -axis.

Table 1

Summary of the function (i.e., meaning) and interpretation of the five parameters found in the two forms proposed, $A(1+(d-1)\exp(-K(t-T_i)/d^{d/(1-d)}))^{1/(1-d)}$ (model (9)) and $A(1+(W_0/A)^{(1-d)}-1)\exp(-Kt/d^{d/(1-d)})^{1/(1-d)}$ (model (14)), plus for the expression for the value (mass or length measurement) at maximum growth rate (i.e., inflection). In these two re-parameterizations (or forms), each parameter controls a single shape characteristic.

Parameter	Function (meaning)	Interpretation
A	Upper asymptote	Adult value
K	Slope at inflection	Maximum relative growth rate ^a
T_i	Time at inflection	Age at maximum growth
$d^{1/(1-d)}$	Proportion of upper asymptote at inflection	Relative value at maximum growth
W_0	Starting value (intersection with the x-axis)	Mass or length at age zero (birth, hatching or germination)

^a The maximum absolute growth rate is therefore KA .

Nahashon et al. (2006) (guinea fowl), and Blicher et al. (2007) (sea urchins). This version is given as

$$A(1+(d-1)\exp(-K(t-T_i)/d^{d/(1-d)}))^{1/(1-d)}. \quad (9)$$

In this form, the d -value no longer affects the growth-rate constant (k), as it is replaced by the actual (relative) growth rate (K). (The d -value still produces sigmoid curves for all values larger than zero.) Thus, each parameter (A , K , T_i , and d) only affects a single curve characteristic (see Table 1), which is an additional improvement from all previously discussed four-parameter model forms.

In addition to the same properties as model (6) (that the inflection point falls at $(T_i, Ad^{1/(1-d)})$, model (9) has the special property that the slope at the inflection point (i.e., the maximum growth rate) is easy to calculate as it becomes AK . Thus, K is the maximum relative growth rate per unit of time (i.e., slope at an inflection). We shall expand our discussion on this model below.

2.3. Common models as special cases of the Richards model

Richards model is a generalization of the negative exponential, the logistic, the von Bertalanffy, and the Gompertz models. For example, the negative exponential model with a location parameter, T_i , (which here gives the intersection with the y -axis) can be given by

$$A(1-\exp(-k(t-T_i))), \quad (10)$$

which is also achieved from Richards model when the exponent is fixed to one, say, when $d=1$ in models (3) through (5) or when $d=0$ in model (6). Likewise for given values of d , the logistic and the von Bertalanffy models become special cases of the Richards model.

The logistic model becomes a special case of the above-mentioned versions of the Richards model, when the exponent is minus one, say, when $d=-1$ in models (3) through (5) and when $d=2$ in model (6). The Richards models then reduces to $A(1-\exp(-k(t-T_i)))^{-1}$, which is the same as (i.e., can be re-parameterized to) the common logistic model on its T_i -form given as

$$A/(1+\exp(-k(t-T_i))). \quad (11)$$

This is the form of the logistic model that is usually given when fitted to plant or animal growth data. Here, T_i gives the time of inflection. Because the inflection value in the Richards model (when the exponent is d) falls at $A/(1-(1/d))^d$, when $d=-1$ for the logistic model, the inflection point for this model falls at $A/(1-(-1))=A/2$ (or 50% of the upper asymptote).

Likewise, the von Bertalanffy model becomes a special case of these versions of the Richards model, when the exponent becomes three. When $d=3$, model (3) reduces to

$$A(1-\exp(-k(t-T_0)))^3, \quad (12)$$

i.e., a Bertalanffy model on the T_0 -form. The von Bertalanffy model is sometimes also given in its T_i -form

$$A(1-(1/3)\exp(-k(t-T_i)))^3, \quad (13)$$

which is derived from Richards model (4) when $d=3$, from model (5) when $d=1/3$, and for model (6) when $d=2/3$. The difference between the two forms of the Bertalanffy model, the T_0 - and the T_i -forms (model (12) and (13)), is often not recognized. We may note that these two models have the same shape, but are shifted horizontally relative to each other. Their inflection value becomes $A/(1-(1/3))^3=8A/27$ (or 29.6% of the upper asymptote). It should also be noted that in the study of fish growth, what is referred to as a “Bertalanffy model” is usually the negative exponential model, $A(1-\exp(-k(t-T_0)))$, whereas in the study of other organisms, for an instance, bird growth, a von Bertalanffy model is typically given as model (12) or (13). We note that for the logistic model (11) the slope at an inflection is $AK/4$, and for the von Bertalanffy model (as given in Eqs. (12) and (13)) the slope at an inflection becomes $AK/3^{3/2}$.

Lastly, the Gompertz model, $A\exp(-\exp(-k(t-T_i)))$, can also be shown to be a special case of Richards model; for example, model (4) will converge towards a Gompertz model when $d \rightarrow \infty$, and model (6) converges toward Gompertz when $d \rightarrow 1$; i.e., in both cases when the inflection value approaches A/e . This convergence is difficult to understand intuitively because the Richards model is not reduced to Gompertz model by simply substituting a given value for d .

2.4. A review of re-parameterizations of the Richards model

Richards' family of models can be re-parameterized in numerous ways. For each model or model form, we shall limit our discussion to only a few examples of re-parameterizations, and provide a more systematic presentation of one lineage of parameterizations (one where the exponent is given as d) in Appendix A. Some of these are more common in the literature than others, and some are even presented under different names. Even the 32 forms (excluding the “compressed” forms) shown in the appendix are not exhaustive, but cover most forms (of one lineage of exponents) found in the literature.

It is not useful to fit two equations that are rearranged, but otherwise exactly identical for the reason that each parameter of the first model has the same meaning as the corresponding parameter in the second model. Therefore, one may want to consult the appendix to see which equations of Richards family are identical. In the appendix, each box (or frame) consists of rearranged versions (of a model) which in effect are identical, so that they not only have the same characteristics, but also have parameters which for a given set of parameter values produce exactly the same curve. All parameterizations are shown for the exponent d (or δ), but may be substituted with $1/d$ or $1/(1-d)$. Likewise, the k -parameter may be substituted with $K/(\text{exponent})$.

2.5. Other superfluous parameterizations and renamed model

Some models found in the literature are merely renamed models of Richards family or parameterizations which contain redundant parameters or terms. For example, the so-called Stannard model given as $A(1+\exp(-k^*(t-c)/d))^{-d}$ (Khamanis et al., 2005; Tsoularis and Wallace, 2002) (where c is a fitted

parameter) is an ordinary Richards model (as noted by [Zwietering et al., 1990](#)), but with the d -parameter in two places instead of one. This is only a re-parameterization of model (2), where k is substituted for k^*/d and c is substituted for $\ln(S)/k$. The new parameters do not describe any single characteristic of curve shape. Therefore, this is neither a “new” model nor a useful re-parameterization.

It is common that models presented as “new” are in fact just re-parameterizations of well known models, or are parameterizations, where curve is lifted or “squeezed” vertically. None of these alternatives should qualify for being “new”. Neither do we believe that these models deserve to be presented or discussed as “new”, when the change only involves a simple transformation or weighting of the independent variable (in this case time or age).

A large number of unnecessary parameterizations and re-parameterizations are found in the literature. Some of these are shown in Appendix A, but many more are possible. A seemingly new complex model is the Richards model found in [Akamine \(2009\)](#), for example. It is given as $A^{1-d} - (A^{1-d} - W_0^{1-d}) \exp(-(1-d)k^*t)^{1/(1-d)}$ which we can rewrite to give $A(1 + ((W_0/A)^{(1-d)} - 1) \exp(-(1-d)k^*t))^{1/(1-d)}$. For the sake of the comparison to model (9), it can also be re-parameterized to give $A(1 + (d-1) \exp(-(1-d)k^*(t - T_i)))^{1/(1-d)}$. In these model versions, the inverse of the exponent (of the Richards model) is substituted for part of the growth constant, so that $k = (1-d)k^*$. It gives to the model the special property of being monotonically increasing and sigmoid only for $0 < d < 1$ (and it always has a starting point on the x -axis). This model, however, only has inflection values between 0 and A/e , which makes it less useful than other versions of Richards model.

3. A unified approach

The review and discussion above of Richards family with its multitude of forms and models point not only to the need, but also to the possibility for standardization (or unification). We propose that the number of standard regression models may be reduced to only two forms (or parameterizations), and that these can replace all other forms and models in this family. The first of these is model (9)

$$A(1 + (d-1) \exp(-K(t - T_i)/d^{d/(1-d)}))^{1/(1-d)}, \quad (9)$$

as described above. This re-parameterization can also be given in the W_0 -form, which means that in a form, where W_0 becomes the intersection value on the y -axis (i.e., at $t=0$)

$$A(1 + ((W_0/A)^{(1-d)} - 1) \exp(-Kt/d^{d/(1-d)}))^{1/(1-d)}, \quad (14)$$

The first of these two forms (or re-parameterizations) of the unified-Richards model, (9), is found previously in the literature; the latter, (14), is not (as far as we know). These two models are especially useful compared to models (6) and (7), in that K becomes maximum relative growth rate, whereas in models (4) and (6) the maximum growth (per unit of time) is $Ad^{d/(1-d)}k$. Thus, $K = d^{d/(1-d)}k$. In effect, in the two proposed parameterizations of Richards model (in the unified approach), each of the five parameters controls a separate shape characteristic. None of the other re-parameterizations has this quality.

In the literature on organismal growth to date, there is a lack of focus on expected shapes and how curve shape found (by regression or curve fitting) can and should be discussed. Typically, only the growth-rate constant (k) is discussed, but it is useful also to discuss other curve characteristics, like the inflection-point placement and the birth or hatching value (which also are helpful in characterizing growth). In the two versions of

Richards model that we advance standards, namely models (9) and (14), these traits are easy to control and discuss. They are represented by [I] maximum (relative) growth rate (i.e., slope at an inflection) (K), [II] age at maximum growth rate (i.e., time at inflection) (T_i), [III] relative mass or length at maximum growth rate (i.e., relative value at an inflection) ($d^{1/(1-d)}$), [IV] value at age zero (i.e., birth, hatching or germination) (W_0), and [V] asymptotic value (i.e., adult weight or length) (A) (see also [Table 1](#)). These five parameters facilitate the unique characterization of any sigmoid-growth data, between any type of different biometric measurement, between populations or between species. The unified-Richards model, therefore, constitutes a powerful tool for the interpretation and characterization of observed growth patterns.

Richards model in general, and the two proposed forms, in particular, are not only flexible, but also constitute a common generalization for several other well known models, including the negative-exponential, the logistic, von Bertalanffy, and Gompertz models. The last three are sigmoid and all have inflection points fixed at a given relative value (i.e., a percentage of the upper asymptote). These three models seem to be those most commonly fitted to growth data of living organisms (as plants, birds, mammals, and more) (see e.g. [Brody, 1945](#); [France and Thornley, 2007](#), for review; [France et al., 1996](#); [Karkach, 2006](#); [Starck and Ricklefs, 1998](#); [Zullinger et al., 1984](#)). Sometimes a fixed inflection point may be useful, for example, when the number of observations is small, and we need to reduce the number of fitted parameters. Instead of applying only these three models, one could derive, for example, from the two proposed forms, a model with an inflection point fixed at any percentage of the upper asymptote. To fix the inflection point at a given value (percentage of the upper asymptote), the appropriate numeral is substituted for the d -parameter in the model. For the two proposed forms, the inflection point is given by (T_i, W_i) , where $W_i = Ad^{1/(1-d)}$. The four-parameter model is thereby reduced to a three-parameter one with a fixed inflection point. [Fig. 2](#) shows the d -value required to fix the inflection point to a given proportion of the upper asymptote.

It is simple to show how some versions of Richards model are generalizations of the logistic model and of von Bertalanffy model, where the logistic model is obtained when the exponent (in Richards model) is minus one and von Bertalanffy model is obtained when the exponent is three. Also, Gompertz model is a special case of Richards model. These three special cases all have fixed relative inflection values. When a sigmoid model for growth data is chosen, the more general Richards model may be preferable, because the placement of the inflection point is

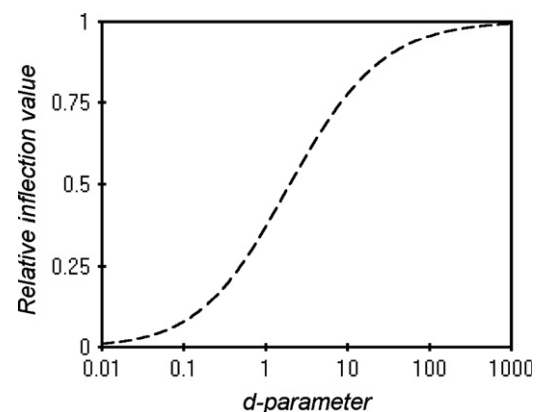


Fig. 2. The graph shows the relationship between the d -parameter the relative inflection value for Richards models (6) and (9), where the exponent is $1/(1-d)$. The inflection value then falls at $W_i = Ad^{1/(1-d)}$. The figure, therefore, shows the relative inflection value as $f(d) = d^{1/(1-d)}$.

flexible. If instead a fixed inflection point is preferred, any placement is possible by the substitution the d -parameter, for a given numerical value. This presents a greater degree of freedom (related to the discussion of curve shape and an inflection-point placement) compared to the choice between candidate models as the logistic, Gompertz, and von Bertalanffy.

4. Model testing

The purpose of our model testing is to assess whether the proposed unified approach, in fact, makes other models in Richards family superfluous. It should match the fit of these rivaling models, each with a different fixed relative inflection value or a different range of inflection values. Therefore, to test the models fitting ability on artificial growth data scatter plot was generated based on each of the five candidate models. We have restricted our model testing to these few data sets and two variations thereof (one with no scatter and one where the upper half of the time sequence is removed). Still, we believe this is sufficient for a first assessment and an indication of the performance of the proposed unified approach.

The artificial data sets were produced for an imaginary species with a birth mass of 4, adult mass of 40, whereof 95% is reached at day 19. (Birth, hatching or germination is set to day one). Standard deviation in growth, e.g. of birds, should be expected to increase after hatching (because of the accumulative effect of environmental differences), and was made therefore to follow $5/(1 + \exp(-0.4t + 2.5))$, where t is number of days since germination, hatching or birth (in agreement with the expectation that variance will increase (following a sigmoid course) after germination, hatching or birth. Also, the situation of no scatter ($SD=0$) was tested. Growth data, e.g. in birds, are generally thought to follow a normal distribution. Normally distributed data sets with 10 observations per day were created for 20 days (including day zero, a total of 200 data point per data set). Data sets were created where averages were based on each of the following models: logistic, Gompertz, Bertalanffy, Richards (1) with $d=1.1$, and Richards (2) with (i) $d=0.5$ and (ii) 0.1 . The d -values were chosen to produce a wide range of inflection-point placements. The model curves were chosen so that the starting point (day 0) was set at 4, the upper asymptote was set at 40, and 95% of the upper asymptote was reached at day 19 (see Appendix B).

Six models were (all) fitted to the artificial data sets: the logistic, Gompertz, Bertalanffy, Richards (1), Richards (2), and the unified-Richards (9) and (14) by nonlinear regression using (the iterative algorithm of) GraphPad Prism version 5.00 for Windows. The upper asymptote was fixed (when fitting all models), as is often done in growth analyses. The asymptote was set to the

same value, as when the artificial data were generated; $A=40$. The results for the two forms (or re-parameterizations) of the unified model were lumped together, because they are identical. The performance of each model was evaluated by the corrected Akaike's Information Criterion (AICc), which penalizes models with a greater number of parameters.

4.1. Statistical performance

The most important is to assure that the unified-Richards model indeed converge with iterative fitting algorithms and indeed return interpretative results. All models returned converged and interpretative results, except in a few cases for the Richards (1) and (2) which resulted in "iteration time-out" (after 1000 iterations) in a few regression runs (The iteration algorithm was probably caught in fitting very small or very large d -values, when the inflection value approached A/e). The unified-Richards model did not outperform all other models for any of the data sets, but it performed well for all data sets; as good, or marginally worse than, the model with the lowest AICc-value (which was defined as the "best" model). Table 2 (and Appendix C for details) shows for which data sets each model was the "best model," i.e., was found to have more than a 25% chance of being the correct model instead of the "best model". For the unified-Richards model, this was the case for all six data sets. No other model achieved this for more than three data sets. This supports the expectation that the two forms of unified-Richards model should be able to substitute all other models and model forms discussed in this paper.

The unified model is expected to perform increasingly better with decreasing scatter (smaller SDs). With no scatter ($SD=0$) only the model the data set is generated from performs as well as the unified-Richards model (Table 3 and Appendix C, the latter for details). We note that the Richards (1) model and the Richards (2), which complement each other in possible placement of the inflection point, even combined were not able to provide as many well fitting curves as the unified model. In these two models "iteration-time-outs" may result if the iteration process (as also occurred here) gets lost trying to calculate extreme d -parameter values (see above). This also speaks in disfavor of Richards (1) and Richards (2) models.

We also ran regressions and applied the AICc to results for shortened data sets, progressively removing the data day by day from the upper timescale. As expected, the results (best fitting model according to the AICc) became more spurious and the models with more parameters (including the unified-Richards model) performed increasingly worse. For example, when only the lower half (first 10 days) of the data set is kept, the number of

Table 2
Performance of the unified-Richards models (9) and (14) compared to five other models, all fitted to the six artificial data sets. The Xs in table mark, where the model has the lowest AICc-value (defined as the "best" model) or has more than 25% of being the correct model rather than the one with the lowest AICc-value, when the standard deviation (SD) follows the described model. The Xs in brackets, (X), mark, where the model has the lowest AICc-value or has more than 0.1% chance of being correct, when $SD=0$.

Dataset based on	Fitted model					
	Logistic	Gompertz	Bertalanffy	Richards (1)	Richards (2)	Unified-R
Logistic	X (X)					X (X)
Gompertz		X (X)	X .	X		X (X)
Bertalanffy		X	X (X)			X (X)
Richards (1)				X (X)		X (X)
Richards (2) i					X (X)	X (X)
Richards (2) ii					X (X)	X (X)

data sets, where the unified model performs best or has more than a 25% chance of being the correct model (instead of the best performing) is reduced from six to five.

4.2. Data requirements

Our results are only an indication of how these models will perform with different empirical data sets, though we believe our artificial data sets cover the typical types of sigmoid-growth data. Still, the usefulness of a given model depends on several properties of the data set. Data requirements are rarely discussed in literature on organismal growth, as there are few clearly defined rules regarding, for example, minimum number of data points and their distribution. It is often assumed that growth data follow a normal distribution. It is, however, when the ordinary least squares (OLS) method is applied, useful to discuss not only normality, but also homoscedasticity of the data, and to consider log-transformation of the predictor (in this case mass, length or volume). Growth data are typically (and should be) sampled across the whole growth period. Pseudoreplication is a general problem with growth data. More than one data point from each individual, or possibly from each sibling, inadvertently results in pseudoreplication, though the seriousness of such may be difficult to judge. There are several ways of avoiding pseudoreplication. One may perform a regression of average values for each day, calculate averages amongst siblings, take random samples from each individual, perform a regression for each individual, or apply a Jackknife method (see also Tjørve et al., 2008). The application of robust regression (which relaxes the assumptions of normality and homoscedasticity) has also become more common and may be a good alternative (see Tjørve et al., 2009, for use of robust regression).

5. Conclusion

The field of organismal growth studies is riddled by a large number of candidate regression models with parameters that are difficult to interpret and to compare. In studies of sigmoidal growth, the growth-rate constant (or growth constant) (k) is typically the only parameter discussed and compared between data sets. For most models, this parameter does not provide a rate, and only provide a parameter value that indicates differences in rate between data sets, which is not directly comparable between models and model versions. We have demonstrated that two specific parameterizations of the Richards model are able to assess growth-curve shape in a systematic and concise manner, and thus unifying and surpassing all other forms and models. Their parameters directly describe curve characteristics that are applicable for the characterization and systematization of growth. In summary, these models exhibit three useful properties:

- Each parameter (A , K , T_i , W_0 , and d) only affects a single curve characteristic.
- The d -parameter moves the inflection value through the whole range 0–100% of the upper asymptote, A .
- The inflection value, W_i , increases continuously with the d -value.

The unified-Richards model is not necessarily best for all types of sigmoid growth and with all data sets. The precedence of the unified-Richards model (over rivaling candidate models) decreases with an increased scatter (larger SDs), if only young (or only old) animals (or plants) are sampled. This is caused both by increased spuriousness and the disadvantage of more parameters than in some rivaling models. Still, the unified model is

Table A1

Genealogy of the Richards family models. The forms in each box behave the same way, and each parameter has the same value for exactly the same course of curve. The preferred form is in bold. The collection of Richards functions can be written not only for (d) as an exponent, but also for $(1/d)$ and $(1/(1-d))$. The two latter opens for new variations (re-parameterizations) over the T_i -form and the T_0 -form (as for example the Richards model $A(1-(1-d)\exp(-k(t-T_i)))^{1/(1-d)}$ can also be written as $A(1+(d-1)\exp(-k(t-T_i)))^{1/(1-d)}$). Also, the compressed form can be written based on any T_i , T_0 or W_0 -forms. Altogether this makes for hundreds of different re-parameterizations of the models in the Richards family. Most of these parameterizations, re-parameterizations, and special cases may be expanded to the two models in this unified approach.

Name	Negative exponential	Logistic	von Bertalanffy	Richards	Richards δ -versions ($\delta = -d$)
T_i -form	n.a.	$A(1+\exp(-k(t-T_i)))^{-1}$	$A(1-(1/3)\exp(-k(t-T_i)))^3$	$A(1-(1/d)\exp(-k(t-T_i)))^d$	$A(1+(1/\delta)\exp(-k(t-T_i)))^{-\delta}$
T_0 -form	$A(1-\exp(-k(t-T_0)))^{-1}$	$A(1+\exp(-k(t-T_i)))$	$A(1-\exp(-k(t-T_0)))^3$	$A(1-\exp(-k(t-T_0)))^d$	$A(1+(1/\delta)\exp(-k(t-T_i)))^{-\delta}$
W_0 -form	$A(1-(1-W_0/A)\exp(-kt))^{-1}$	n.a.	$A(1-(1-(W_0/A)^{1/3})\exp(-kt))^3$	$A(1-(1-(W_0/A)^{1/d})\exp(-kt))^d$	n.a.
	$A(1+(W_0/A-1)\exp(-kt))^{-1}$	$A(1+(A/W_0-1)\exp(-kt))^{-1}$	$A(1+((W_0/A)^{1/3}-1)\exp(-kt))^3$	$A(1+((W_0/A)^{1/d}-1)\exp(-kt))^d$	$A(1+(A/W_0)^{1/\delta}-1)\exp(-kt))^{-\delta}$
	$A(1-(A-W_0/A)\exp(-kt))$	$A(1-(A^{-1}-W_0^{-1})/A^{-1}\exp(-kt))^{-1}$	$A(1-(A^{1/3}-W_0^{1/3})/A^{1/3}\exp(-kt))^{-1}$	$A(1-(A^{1/d}-W_0^{1/d})/A^{1/d}\exp(-kt))^{-d}$	$A(1+(A^{1/\delta}-W_0^{1/\delta})/A^{1/\delta}\exp(-kt))^{-\delta}$
	$A(1+((W_0-A)/A)\exp(-kt))$	$A(1+((W_0^{-1}-A^{-1})/A^{-1})\exp(-kt))^{-1}$	$A(1+((W_0^{1/3}-A^{1/3})/A^{1/3})\exp(-kt))^{-1}$	$A(1+((W_0^{1/d}-A^{1/d})/A^{1/d})\exp(-kt))^{-d}$	$A(1+(A^{1/\delta}-W_0^{1/\delta})/A^{1/\delta}\exp(-kt))^{-\delta}$
	$A(1-(W_0-A)\exp(-kt))$	$A(1-(A^{-1}-W_0^{-1})\exp(-kt))^{-1}$	$A(1-(A^{1/3}-W_0^{1/3})\exp(-kt))^{-1}$	$A(1-(A^{1/d}-W_0^{1/d})\exp(-kt))^{-d}$	$A(W_0/W_0^{1/\delta}-(W_0^{1/\delta}-A^{1/\delta})\exp(-kt))^{-\delta}$
	$(A+W_0-A)\exp(-kt)$	$(A^{-1}+W_0^{-1}-A^{-1})\exp(-kt)^{-1}$	$(A^{1/3}+W_0^{1/3}-A^{1/3})\exp(-kt)^{-1}$	$(A^{1/d}+W_0^{1/d}-A^{1/d})\exp(-kt)^{-d}$	$A(W_0/W_0^{1/\delta}+(A^{1/\delta}-W_0^{1/\delta})\exp(-kt))^{-\delta}$
	$A(1-1-W_0/A)\exp(-kt)^{-1}$	$A(1-1-W_0/A)\exp(-kt)$	$A(1-(1-(W_0/A)^{1/3})\exp(-kt))^{-3}$	$A(1-(1-(W_0/A)^{1/d})\exp(-kt))^{-d}$	$A(1-(1-(A/W_0)^{1/\delta})\exp(-kt))^{-\delta}$
	$A(1+(W_0/A-1)\exp(-kt))^{-1}$	$A(1+(W_0/A)^{1/3}-1)\exp(-kt)^{-3}$	$A(1+(W_0/A)^{1/3}-1)\exp(-kt)^{-3}$	$A(1+((W_0/A)^{1/d}-1)\exp(-kt))^{-d}$	$A(1+(A/W_0)^{1/\delta}-1)\exp(-kt))^{-\delta}$
	$A(1-(A-W_0)/W_0)\exp(-kt))^{-1}$	$A(1-(A-W_0)/W_0)\exp(-kt)$	$A(1-(A^{1/3}-W_0^{1/3})/A^{1/3})\exp(-kt))^{-3}$	$A(1-(A^{1/d}-W_0^{1/d})/A^{1/d})\exp(-kt))^{-d}$	$A(1-(W_0^{1/\delta}-A^{1/\delta})/W_0^{1/\delta})\exp(-kt))^{-\delta}$
	$A(1+((W_0-A)/A)\exp(-kt))^{-1}$	$A(1+((W_0^{-1}-A^{-1})/W_0)\exp(-kt))^{-1}$	$A(1+((W_0^{1/3}-A^{1/3})/A^{1/3})\exp(-kt))^{-3}$	$A(1+((W_0^{1/d}-A^{1/d})/A^{1/d})\exp(-kt))^{-d}$	$A(1+(A^{1/\delta}-W_0^{1/\delta})/W_0^{1/\delta})\exp(-kt))^{-\delta}$
	$1/(A-(A-W_0)\exp(-kt))^{-1}$	$1/(A^{-1}-(A^{-1}-W_0^{-1})\exp(-kt))$	$1/(A^{1/3}-(A^{1/3}-W_0^{1/3})\exp(-kt))^{-3}$	$1/(A^{1/d}-(A^{1/d}-W_0^{1/d})\exp(-kt))^{-d}$	$A(W_0/(W_0^{1/\delta}-(W_0^{1/\delta}-A^{1/\delta})\exp(-kt))^{-\delta}$
	$1/(A+(W_0-A)\exp(-kt))^{-1}$	$1/(A^{-1}+(W_0^{-1}-A^{-1})\exp(-kt))$	$1/(A^{1/3}+(W_0^{1/3}-A^{1/3})\exp(-kt))^{-3}$	$1/(A^{1/d}+(W_0^{1/d}-A^{1/d})\exp(-kt))^{-d}$	$A(W_0/(W_0^{1/\delta}+(A^{1/\delta}-W_0^{1/\delta})\exp(-kt))^{-\delta}$
	n.a.	$B+(A-B)(1+\exp(-k(t-T_i)))^{-1}$	$B+(A-B)(1-(1/3)\exp(-k(t-T_i)))^3$	$B+(A-B)(1-(1/d)\exp(-k(t-T_i)))^d$	$B+(A-B)(1+(1/\delta)\exp(-k(t-T_i)))^{-\delta}$
Compr. T_i -form	n.a.	$B+(A-B)(1+\exp(-k(t-T_i)))$	$B+(A-B)(1-(1/3)\exp(-k(t-T_i)))^3$	$B+(A-B)((1-(1/3)\exp(-k(t-T_i)))^{-3}$	$B+(A-B)((1+(1/\delta)\exp(-k(t-T_i)))^{-\delta}$

certainly, with reasonably good data sets, expected to be able to cover a broader spectrum of curve shapes better overall than any of the other models we have reviewed in this paper. We believe, rooted in both useful behavior and wide fitting ability, a new standard based on the two proposed model forms can facilitate more complete, more precise, and more comparable research that will benefit future studies.

Table B1

The “mean values” and “standard deviations (SD)” for the artificial data sets are based on a chosen set of model curves. The mean values are taken at every integer (of t) from 0 to 19 for six model curves (given below), representing five rivaling candidate models. The SD for the mean values was then made to follow $5/(1+\exp(-0.4t+2.5))$. From these (means and SDs) six artificial data sets with 10 random normally distributed values were generated for each mean value (producing 200 data points in each data set).

Model	Curve the data set is based on
Logistic	$40/(1+\exp(-0.271(t-8.12)))$
Gompertz	$40 \exp(-\exp(-0.200(t-4.17)))$
Bertalanffy	$40(1-\exp(-0.182(t+3.429)))^3$
Richards (1)	$40(1-0.8767 \exp(-0.1556t))^{1.1}$
Richards (2) i	$40/(1+99 \exp(-0.359t))^{0.5}$
Richards (2) ii	$40/(1+10^{10} \exp(-1.233t))^{0.1}$

Table C1

Differences in corrected values for Akaike's Information criterion between the best performing model and the other candidate models fitted to the six artificial data sets. The table shows which type of curve (model) the dataset is generated from, which model was fitted, the AICc difference between this model and the “best” model (defined as the one with the lowest AICc-value), and the probability this model is better than the “best”. Results are shown for standard deviation (SD) modeled from $5/(1+\exp(-0.4t+2.5))$ and for SD=0.

Data set from	Model fitted	SD modeled		SD=0	
		AICc diff.	Prob. correct ^a	AICc diff.	Prob. correct ^a
Logistic curve	<i>Logistic</i>	0.00	BEST	2.79	0.1984
	<i>Gompertz</i>	17.29	0.0002	2360.33	0.0000
	<i>Bertalanffy</i>	33.33	0.0000	2512.59	0.0000
	<i>Richards (1)</i>	19.44	0.0001	2362.51	0.0000
	<i>Richards (2)</i>	1.85	0.2834	0.00	BEST
	<i>Unified-Richards</i>	1.85	0.2834	0.00	BEST
Gompertz curve	<i>Logistic</i>	18.24	0.0001	2475.36	0.0000
	<i>Gompertz</i>	0.00	BEST	4.76	0.0848
	<i>Bertalanffy</i>	0.99	0.3782	2165.81	0.0000
	<i>Richards (1)</i>	1.85	0.2837	(Iteration-time-out)	
	<i>Richards (2)</i>	3.15	0.1713	(Iteration-time-out)	
	<i>Unified-Richards</i>	1.85	0.2837	0.00	BEST
Bertalanffy curve	<i>Logistic</i>	20.92	0.0000	2550.28	0.0000
	<i>Gompertz</i>	1.94	0.2745	2087.08	0.0000
	<i>Bertalanffy</i>	0.00	BEST	12.23	0.0022
	<i>Richards (1)</i>	37.83	0.0000	2331.78	0.0000
	<i>Richards (2)</i>	3.95	0.1221	(Iteration-time-out)	
	<i>Unified-Richards</i>	2.08	0.2609	0.00	BEST
Richards (1) curve	<i>Logistic</i>	24.34	0.0000	3397.69	0.0000
	<i>Gompertz</i>	5.84	0.0512	3188.59	0.0000
	<i>Bertalanffy</i>	24.64	0.0000	3523.47	0.0000
	<i>Richards (1)</i>	0.00	BEST	0.00	BEST
	<i>Richards (2)</i>	7.92	0.0187	3190.67	0.0000
	<i>Unified-Richards</i>	0.00	BEST	83.07	BEST
Richards (2) i	<i>Logistic</i>	3.57	0.1435	3217.33	0.0000
	<i>Gompertz</i>	38.35	0.0000	3593.71	0.0000
	<i>Bertalanffy</i>	61.71	0.0000	3692.18	0.0000
	<i>Richards (1)</i>	40.50	0.0000	3595.85	0.0000
	<i>Richards (2)</i>	0.00	BEST	0.00	BEST
	<i>Unified-Richards</i>	0.00	BEST	0.00	BEST
Richards (2) ii	<i>Logistic</i>	29.17	0.0000	3662.87	0.0000
	<i>Gompertz</i>	73.02	0.0000	3820.96	0.0000
	<i>Bertalanffy</i>	95.76	0.0000	3876.18	0.0000
	<i>Richards (1)</i>	80.71	0.0000	3823.04	0.0000
	<i>Richards (2)</i>	0.00	BEST	0.00	BEST
	<i>Unified-Richards</i>	0.00	BEST	0.00	BEST

^a Only the unified-Richards model performs acceptable (or indeed is “best”) with data sets based on all curve models.

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Appendix A

Table A1.

Appendix B

Table B1.

Appendix C

Table C1.

References

- Aggrey, S.E., 2002. Comparison of three nonlinear and spline regression models for describing chicken growth curves. *Poultry Science* 81, 1782–1788.
- Aggrey, S., Ankra-Badu, G., Marks, H., 2003. Effect of long-term divergent selection on growth characteristics in Japanese quail. *Poultry Science* 82, 538–542.
- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19, 716–723.
- Akamine, T., 2009. Non-linear and graphical methods for fish stock analysis with statistical modelling. *Aqua-BioScience Monographs* 2, 1–45.
- Bertalanffy, v.L., 1938. A quantitative theory of organic growth. *Human Biology* (10), 181–213.
- Blicher, M.E., Rysgaard, S., Sejr, M.K., 2007. Growth and production of sea urchin *Strongylocentrotus droebachiensis* in a high-Arctic fjord, and growth along a climatic gradient (64–77°N). *Marine Ecology Progress Series* 341, 89–102.
- Brody, S., 1945. *Bioenergetics and Growth*. Hafner, New York.
- Chapman, D.G., 1961. Statistical problems in population dynamics of exploited fisheries populations. *Proceedings of the Fourth Berkely Symposium—Mathematical Statistics and Probability Proceedings*. University of California Press, Berkeley, pp. 153–168.
- France, J., Thornley, J.H.M., 1984. *Mathematical Models in Agriculture: a Quantitative Approach to Problems in Agriculture and Related Sciences*. Butterworth, London.
- France, J., Thornley, J.H.M., 2007. *Mathematical Models in Agriculture: Quantitative Methods for the Plant, Animal and Ecological Sciences*. CABI, Oxon, UK.
- France, J., Dijkstra, J., Dhanoa, M.S., 1996. Growth functions and their application in animal science. *Annales de Zootechnie* 45 (Suppl.), 165–174.
- Frie, A., Potelov, V., Kingsley, C., Haug, T., 2003. Trends in age-at-maturity and growth parameters of female Northeastern harp seals, *Pagophilus groenlandicus* (Erxleben, 1777). *ICES Journal of Marine Science* 60, 1018–1032.
- Gompertz, B., 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 182, 513–585.
- Karkach, A.S., 2006. Trajectories and models of individual growth. *Demographic Research* 15, 347–400.
- Khamanis, A., Ismail, Z., Haron, K., Mohammed, A.T., 2005. Nonlinear growth models for modeling oil palm yield growth. *Journal of Mathematics and Statistics* 1, 225–233.
- Krafft, B., Kovacs, K., Frie, A., Haug, T., C, L., 2006. Growth and population parameters of ringed seals (*Pusa hispida*) from Svalbard, Norway, 2002–2004. *ICES Journal of Marine Science* 63, 1136–1144.
- Nahashon, S., Aggrey, S., Adefope, N., Amenyenu, A., Wright, D., 2006. Growth characteristics of Pearl Gray Guinea Fowl as predicted by the Richards, Gompertz and logistic models. *Poultry Science* 85, 359–363.
- Pienaar, L.V., Turnbull, K.J., 1973. The Chapman–Richards generalization of von Bertalanffy's growth model for basal area growth and yield in even-aged stands. *Forest Science* 19, 2–22.
- Ratkowsky, D.A., 1983. *Nonlinear Regression Modelling: a Unified Approach*. Marcel Dekker, New York.
- Richards, F.J., 1959. A flexible growth function for empirical use. *Journal of Experimental Botany* 10, 290–300.
- Richards, F.J., 1969. The quantitative analysis of growth. In: Steward, F.C. (Ed.), *Plant Physiology*. Academic Press, New York, pp. 3–76.
- Schnute, J., 1981. A versatile growth model with statistically stable parameters. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 1128–1140.
- Schwarz, G.E., 1978. Estimating the dimension of a model. *Annals of Statistics* 6, 461–464.
- Starck, J.M., Ricklefs, R.E., 1998. Variation, constraint, and phylogeny: comparative analysis of variation in growth. In: Starck, J.M., Ricklefs, R.E. (Eds.), *Avian Growth and Development*. Oxford University Press, Oxford, pp. 247–265.
- Sugden, L.G., Driver, E.A., Kingsley, M.C.S., 1981. Growth and energy consumption by captive mallards. *Canadian Journal of Zoology* 59, 1567–1570.
- Tjørve, E., 2003. Shapes and functions of species-area curves: a review of possible models. *Journal of Biogeography* 30, 827–835.
- Tjørve, E., 2009. Shapes and functions of species-area curves (II): a review of new models and parameterizations. *Journal of Biogeography* 36, 1435–1445.
- Tjørve, K., Underhill, L., Visser, G., 2008. The energetic implications of precocial development of shorebirds breeding in a warm environment. *Ibis* 150, 125–138.
- Tjørve, K.M.C., Underhill, L.G., Visser, G.H., 2009. Growth, sibling rivalry and their relationship to fledging success in African Black Oystercatchers *Haematopus moquini*. *Zoology* 112, 27–37.
- Tsoularis, A., Wallace, J., 2002. Analysis of logistic growth models. *Mathematical Biosciences* 179, 21–55.
- Verhulst, P.F., 1838. Notice sur la loi que la population suit dans son accroissement. *Correspondences Mathématiques et Physiques* 10, 113–121.
- Zullinger, E.M., Ricklefs, R.E., Redford, K.H., Mace, G.M., 1984. Fitting sigmoidal equations to mammalian growth rates. *Journal of Mammalogy* 65, 607–636.
- Zwietering, M.H., Jongenburger, I., Rombouts, F.M., 1990. Modeling of the bacterial growth curve. *Applied and Environmental Microbiology* 56, 1875–1881.