Research paper

A proposed family of Unified models for sigmoidal growth

Kathleen M.C. Tjørve *, Even Tjørve

Inland Norway University of Applied Sciences, P.O. Box 400, 2418 Elverum, Norway

ABSTRACT

The four-parameter Unified Richards model has been applied to the growth of different animal taxa. Traditionally researchers of animal growth have favoured three-parameter models such as the logistic, Gompertz, and von Bertalanffy models. However, the growth-rate parameters of the traditional versions of these models are incomparable, and model forms returning starting points for the curves are not available. Therefore, we have reviewed and developed the family of Unified growth models (U-models), including U-versions of the logistic, Gompertz, and von Bertalanffy models, which each have an inflection placement at a fixed percentage of the upper asymptote. Consequently, in order to accommodate for those who prefer a three-parameter model, we also deduce (show) how to derive from the U-Richards a new, generic, three-parameter U-models with any predetermined inflection placement. This means an indefinite number of U-models, which will cover inflection placements at any percentage of the upper asymptote. All U-models have been re-parameterized to exhibit a unified set of parameters, which measure the same thing cross all family members, hence these models are termed the Unified family (or simply U-family). We also discuss how to interpret parameter values and whether to restrain the asymptote to a fixed value. All U-family models can be fitted to data in either of two forms: the first where one of the parameters represents the time of inflection, and the second with a parameter representing the starting value (intersection with the x-axis). Each parameter in these models only affects a single curve-shape characteristic. We show, also by fitting the models to bird growth data, how only a complete U-Richards family of models and accompanying parameter-translation equations will guarantee that we will be able to choose a model that returns realistic values and provides a consistent interpretation of growth data. There should be no enticement to choose other tools for analysing sigmoidal growth. Traditional versions of the Gompertz, logistic, von Bertalanffy or Richard's models found in the literature have various shortcomings.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Many types of biological growth, including human and animal, are typically studied by fitting sigmoid nonlinear regression models to a time series of measurements (size, mass, or length). Understanding which models best describe the growth trajectory, both empirically and mechanistically, is a great challenge. Numerous models and techniques for fitting regressions to growth data have been adopted by different fields in order to describe growth; and developments in one field have not necessarily been transferred to others. This is understandable, since the growth literature is immense.
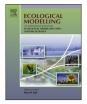
Models of biological growth go all the way back to (Gompertz, 1825) when Gompertz modelled human mortality (life

expectancy), although the first to apply Gompertz' growth model to biological growth data was probably Davidson (1928) who studied body-mass growth in cattle. However, the logistic model, which was introduced by Verhulst (1845) in the study of population growth, was applied to bacterial growth already by McKendrick and Pai (1912). It was not until the 1940s, however, that (ordinary least squares) regression was applied to fit these and other sigmoid models with an upper asymptote (and Hartley, 1948; see e.g. Stoner, 1941).

Today, growth is typically studied by fitting a sigmoid regression model with an upper asymptote to data by means of non-linear regression, usually by the use of the ordinary least-squares method. More recently, alternative methods have become available, such as (hierarchical) nonlinear mixed models (Aggrey, 2009; Sofaer et al., 2013), robust (non-parametric) regression (e.g. Tjørve et al., 2009), and spline (piecewise) regression models (Aggrey, 2002; Brown et al., 2007; Vitezica et al., 2010), the latter being an alternative to the fitting of traditional growth models. A main caveat, to the fitting

of traditional regression models and comparisons between models or between studies using different models, is that the parameters are not comparable. Until now, no known set of models has parameters that are all directly comparable.

The primary purpose of this article is to review and develop a family of models, the U-family, as well as to establish a conceptual foundation for their use. The U-family models have been re-parameterized to exhibit a unified set of parameters across three parameter models (the logistic, Gompertz, and von Bertalanffy models) and one four-parameter model (the Richards model), where the latter is a generalization of the three other models. We suggest calling this family of Unified models (U-models) the Unified family, or simply the U-family. Henceforth, we use the term "unified" on such a set of parameters where each parameter has the same meaning, i.e. measures of the same thing, in all models, and each parameter only affects one curve-shape characteristic. For each model, we will present two model forms, which differ in type of location parameter. We shall also provide translation equations between the two location parameters of the different U-models.

We will further discuss the inflection values and growth coefficients of these models and how these have been, and should be, used. The purpose of this article is, therefore, to propose a complete U-family of models, and show how this and accompanying parameter-translation equations allow for a consistent interpretation of growth data, generating comparable metrics across all models. We will also fit these models to three sets of data (our own bird-growth data), to illustrate the usefulness of the generic three-parameter model (which may replace the use of the U-Richards, when a three-parameter model is preferred). This may illustrate the advantages of a consistent family of models, where all parameter values can be compared directly. We have tried to write this article so that the methods and advancements may be easily comprehended and adopted by the empiricist, in addition to the practicing field ecologist or physiologist.

2. Three-parameter models

Sigmoid regression models with three-parameters and upper asymptotes are fitted to many types of biological growth. The most widely used models are the logistic, Gompertz, and von Bertalanffy (see Appendix A for some common model versions of these), which are related and behave similarly.

These models appear in a multitude of versions or re-parameterisations, and sometimes different models (or nested models, which cannot be regarded as merely re-parameterizations) are found under the same name (as for example "von Bertalanffy" models decribed by Beverton and Holt, 1957; and by Ricklefs, 1975). Researchers studying growth in farm animals (poultry and livestock) have increasingly used a re-parameterization of the Gompertz, referred to as the Gompertz-Laird model (Laird, 1969), much owing to Aggrey's (2002) article describing chicken growth. Fish researchers have also used the Gompertz-Laird model when studying growth of fish larvae (early developmental stages of fish) and otoliths (Narimatsu et al., 2007). However, they have mostly fitted Ricker's (1979) re-parameterization of the Gompertz-Laird. The von Bertalanffy model has also been fitted to fish growth (e.g. Cailliet et al., 2006; Chen et al., 1992), but often in a form given by Beverton and Holt (1957), which is different to that used for bird growth (see Ricklefs, 1967, 1975). Although invertebrate growth has often been modelled using the exponential (Hirst and Bunker, 2003; Nylin, 1992) or the power (allometric) (Tammaru and Esperk, 2007) functions, it has more recently been described using re-parameterisations of the von Bertalanffy model; for example the growth of jellyfish (Palomares and Pauly, 2009) and mussels (Anthony et al., 2001). As Ricker's (1979) book heav-

ily influenced studies of fish growth, so have Ricklefs (1967, 1968, 1975) articles shaped the study of bird growth. Bird growth has been described using the von Bertalanffy (as in fish and invertebrates), but the logistic and the traditional Gompertz models are also commonly used. These three sigmoidal models have also been popular in describing the growth of mammals (Zullinger et al., 1984; Palomares and Pauly, 2008). The Gompertz, logistic and von Bertallanffy models have, amongst other models, been used to describe the growth of algae (Halmi et al., 2014) and plants (see Karkach, 2006, for review). Although determinate growth models like the Gompertz, logistic and von Bertalanffy, do not always optimally describe plant growth, the logistic model has been used to describe crop and weed growth (Yin et al., 2003; Karlsson and Milberg, 2007; Chauhan and Johnson, 2011).

It is important to note that many of the model re-parameterisations found in the literature are not useful, either because the parameters affect more than one shape characteristic making it difficult to compare parameters, or because the parameters do not generate directly interpretable values (see Tjørve and Tjørve, 2010b; Tjørve and Tjørve, in press; Tjørve and Tjørve, 2016).

There are some studies that have addressed the selection of growth curves (e.g. Aggrey, 2002; Brisbin et al., 1987; Ricklefs, 1967; Tjørve and Tjørve, 2010b; Zach, 1988; Zweitering et al., 1990). Surprisingly little attention has been given to the trajectories that may preclude the use of these models (Zach, 1988). For example, in bird post-natal growth, some species reach adult body mass long after fledging (Beintema and Visser, 1989; Reed et al., 1999; Tjørve et al., 2007; Tjørve et al., 2008, 2009), whereas young of other species reach a peak mass before fledging (e.g.Huntington et al., 1996) followed by weight loss to reach adult mass after fledging (but see Huin and Prince, 2000). Both patterns may cause unrealistic values for fitted asymptotes.

The behaviour and products of the commonly used growth models have not been thoroughly explored: this includes their ability to indicate negative growth rates, the accuracy of estimated confidence intervals, and the accuracy of the predicted asymptotes (Brisbin et al., 1987; Brown et al., 2007; Remeš and Martin, 2002; Zach, 1988). Clearly these commonly used growth models do not have a maximum to enable the modelling of species whose mass decreases after fledging. A model which could describe sigmoid growth with a maximum followed by negative growth and then levelling off would be complex. Therefore, a discussion of growth-curve model selection is needed, and one needs to fit growth models that both fit the data and give biologically meaningful growth curves.

3. The Richards and U-Richards

The Richards' (1959) model was first suggested for plant data (as F.J. Richards was a plant physiologist of the Imperial College of Science in London). Some re-parameterizations have also gone under the name of the Chapman-Richards model (Pienaar and Turnball, 1973; Ratkowsky, 1990). It is very similar to von Bertalanffy's (1938, 1957) four parameter model, and the Richards model is sometimes referred to as the von Bertalanffy or the Bertanlanffy-Richards. Today a von Bertalanffy model is usually a three-parameter model (with an exponent of either one or three).

The Richards model is the natural alternative to the traditional three-parameter models. However, it was not until about 1980 that it became more commonly fitted to biological growth data. Soon it was fitted to everything from epidemics (Madden, 1980) to growth in birds (Sugden et al., 1981; White and Brisbin Jr, 1980; White and Ratti, 1977), alligators (Jacubsen and Kushlan, 1989), mammals (Leberg et al., 1989), or plants (Venus and Causton, 1978), including the height of forest stands (Garcia, 1983). Several critical contribu-