

# A review on fish growth calculation: multiple functions in fish production and their specific application

Vincent Lugert<sup>1</sup>, Georg Thaller<sup>1</sup>, Jens Tetens<sup>1</sup>, Carsten Schulz<sup>1,2</sup> and Joachim Krieter<sup>1</sup>

<sup>1</sup> Institute of Animal Breeding and Husbandry, Christian-Albrechts-University, Kiel

<sup>2</sup> GMA – Gesellschaft für Marine Aquakultur mbH, Büsum, Germany

## Correspondence

Mr Vincent Lugert, Christian-Albrechts-University Kiel, Institute of Animal Breeding and Husbandry, Olshausenstr. 40, 24098 Kiel, Germany. Email: vlugert@tierzucht.uni-kiel.de

Received 18 March 2014; accepted 17 July 2014.

## Abstract

Modern aquaculture recirculation systems (RASs) are a necessary tool to provide sustainable and continuous aquaculture production with low environmental impact. But, productivity and efficiency of such RAS still have to be optimized to ensure economic viability, putting growth performance into the focus. Growth is often reported as absolute (gain per day), relative (percentage increase in size) or specific growth rate (percentage increase in size per day), based on stocking and harvesting data. These functions describe growth very simplified and are inaccurate because intermediate growth data are not considered. In contrast, nonlinear growth models attempt to provide information of growth across different life stages. On the basis of an empirical RAS data set of 150 all-female turbot reared in an RAS during a period of 340 days of outgrowth, this paper reviews the most commonly used growth rates (relative, absolute, specific), the thermal-unit growth coefficient and five nonlinear growth functions (logistic, Gompertz, von Bertalanffy, Kanis and Schnute). Goodness of fit is expressed by  $R^2$  and as mean percentage deviation. Nonlinear growth models are also compared by their residual standard error (RSE) and the Akaike information criterion. All processed functions are modelled to illustrate the shape of the generated curve and the possibility of the function to realistically predict growth. Further, the biological meaning of their regression parameters is discussed. This way we can point out differences in nonlinear growth models in contrast to purely descriptive growth rates and the specific advantages, disadvantages and possible applications of each function we review.

**Key words:** aquaculture, growth, growth function, model, von Bertalanffy.

## Introduction

The capacity of marine wild stock fishing has stagnated at about 80 million tons per year (FAO 2012) over the last decade. This stagnation in world fisheries is accompanied by a growing world population and a growing demand of fish as a high-quality protein food source. To satisfy the increasing demand on seafood, aquaculture has gained serious interest in the past and the scene has obtained a major role in supplying the market with fresh seafood. Aquaculture production of fish, crustaceans and molluscs has become the world's fastest-growing food-producing industry (Klinkhardt 2011) with an annual growth of approximately 8% (FAO 2012). Due to the resulting impacts to the surrounding environment paired with occurring social

problems, open aquaculture production obtained more environmental restrictions within the last years. Modern recirculation aquaculture systems (RASs) have become an important tool to provide sustainable, environmental-friendly and constant aquaculture production. As these systems require high investment and operating costs, they need to be highly productive to sustain profit whereas the growth of the produced organisms is the major challenge.

Growth is in unison defined as a gradual increase in a living system in some quantity over time (e.g. Von Bertalanffy 1934). In commercial aquaculture facilities, the growth performance of organisms is the most important influencing factor with regard to economic benefit (Baer *et al.* 2010). As rate of growth in weight approaches the reflection point, the economic return of fish yield at harvest increases

(Springborn *et al.* 1994); afterwards, it decreases. For rearing purposes, it is crucial to know the limits of growth because the growth of fish in aquaculture production systems differs from the growth of fish in the wild (Baer *et al.* 2010). Growth of fish underlies a wide range of positive or negative impacting factors. In fish, growth mainly depends on feed consumption and quality (e.g. Rosenlund *et al.* 2004; Slawski *et al.* 2011); stocking density (Ma *et al.* 2006); biotic factors such as sex (e.g. Déniel 1990; Imsland & Jonassen 2003) and age (e.g. Von Bertalanffy 1938; Déniel 1990); genetics variance; and abiotic factors such as water chemistry, temperature (e.g. Karås & Klingsheim 1997; Imsland *et al.* 2007a,b), photoperiod (e.g. Imsland & Jonassen 2003) and oxygen level (Brett 1979).

Growth functions are mathematical equations used to express the increase in body dimensions over time. Aquaculturists typically report growth using absolute (weight gain per time), relative (percentage increase in body weight) and specific growth rates (percentage increase in body dimension per time) (Hopkins 1992), calculated only on the basis of the stocking and harvest data, and do not consider growth within this period. Thus, intermediate data are unconsidered or even lost (Hopkins 1992). Because of their mathematical simplicity, these functions can only describe the observed growth process during an ongoing study, which is very simplified. They cannot precisely extend beyond empirical data and are therefore not able to make any prediction about further growth development. Nevertheless, because of their simple appliance, comparability of results and biological interpretation these functions have become the most frequently used functions in aquaculture publications. In fishery science and biomathematics, there have been long-lasting and intensive efforts to provide and test a large amount of different nonlinear growth functions to exactly specify growth of different aquatic species (e.g. Gompertz 1825; Pütter 1920; Von Bertalanffy 1934, 1938; Brody 1945; Krüger 1965, 1973; Hohendorf 1966). Mostly, these functions are used for calculations on wildlife stock, the interpretation of habitat or the comparison of nutrition studies. Nonlinear growth model uses regression parameters to describe the shape of the generated curve. In contrast, in polynomial functions, which may even gain a better fit to a given data set, regression parameters have no independent biological meaning if they are not orthogonalized (e.g. Von Bertalanffy 1934; Brody 1945; Richards 1959; Ricker 1979; Parks 1982; Kanis & Koops 1990). Additionally, when using polynomials, extrapolation is not allowed, limiting their application to intermediate data (Kanis & Koops 1990). Nonlinear models can be classified into functions of multiple possible shapes: functions describing exponential, bounded (or diminishing returns behaviour/diminishing exponential) or a sigmoidal shape (López *et al.*, 2000). Such functions of bounded or sigmoidal shape

arise towards a mathematically fixed asymptote (e.g. logistic, Gompertz, Richards, von Bertalanffy). As asymptotic growth is proven to be the case in many fish species (Hohendorf 1966; Katsanevakis & Maravelias 2008), such functions are frequently used to estimate growth (Krieter & Kalm 1989; Déniel 1990; Baer *et al.* 2010; Hernandez-Llomas & Ratkowsky 2004). Ricker (1979) points out that an average asymptotic size is estimated whether there will always fish appear that grow considerably larger or smaller than the average. Though, the estimated asymptote of the regression can be used for biological interpretation. Further, the point of inflection (POI) as well as function-specific growth parameters (e.g.  $k$ ) can be used for biological interpretation. Therefore, not only the goodness of fit of a certain function but also the shape of the generated curve as well as the regression parameters must be considered to evaluate the best model for a certain data set. Today, scientists use growth functions in an attempt to provide reliable background information for repeatable results and as basis for management decisions on aquaculture systems. Such mathematical models have proven great suitability for collected data and are labelled indispensable in estimating growth as one of the major interests in animal production (Dumas *et al.* 2010). Especially in RAS, where conditions for the reared organisms are assessable and constantly stagnant, nonlinear growth models can achieve great match with the collected data, and it is therefore incomprehensible why nonlinear models are so infrequently used. Also, the von Bertalanffy growth function (VBGF) has often been chosen to be the optimal model for the data set before even testing others, perhaps even more suitable growth models (Baer *et al.* 2010), as finding the function that provides the optimal fit for the data set can require considerable mathematical, statistical and time effort.

It has to be an attempt of both aquaculturists and scientists, to know about growth functions and their unique advantages and disadvantages in terms of the specific application. To establish easy-to-use, species-fitted nonlinear growth models as standard methods in aquaculture can therefore be a key factor for increasing the efficiency of RAS facilities.

On the basis of an empirical data set of all-female turbot (cf. example data set) from an RAS system, this work focuses on the specific application of the common growth functions, general difficulties and advantages and intends to reveal the need of well-fitted nonlinear models in aquaculture. We intend to disclose the differences between pure descriptive functions (growth rates) and more complex function (growth models) that are able to simulate the future growth process of the actual stock. Furthermore, we want to encourage aquaculturists to use the most appropriate function for their data by reviewing, calculating and comparing the linear and exponential standard methods

and some nonlinear curves on the basis of the same data set. This way we can show the differences between each function and the possibility of exact and most realistic prediction of fish growth in aquaculture under the use of the best-fitting and most realistic function. Exact prediction of fish individual growth or stock development is a key for stock assessment, harvest planning, feeding cost calculation and production period, as well as marketing management in a viable RAS facility.

To fully understand the range and importance of this topic, it is crucial to know about the physiological background and laws of growth of cold-blooded animals. As this is a very wide subject, here it will only be processed in its basics to provide some information on the following work. Hesse (1927) mentioned that the surface area of the intestine canal is, in proportion to the body mass, much larger in young fish than it is in older fish. Because of the correlation between absorbed nutrients and the expanded observing surface, younger fish have growth advantages regarding diet if enough food is available (Von Bertalanffy 1934). This way they can absorb more nutrients than they exhaust and can invest the remaining excess into growth. This excess decreases by steady body increase, because of the shrinking proportion of intestine surface to body mass (Von Bertalanffy 1934) and the increasing energy demand of the animal. As a result, fish growth decreases until finally a balance of absorbed nutrition (anabolism) and energy consumption (catabolism) is reached. The effect of increasing or asymptotic growth, resulting in an S-shaped sigmoid growth curve, is additionally forced, when the animal reaches sexual maturity, because an increasing amount of energy is invested in gonad production. Dumas *et al.* (2010) point out that the growth process of the above-described biological growth trajectories can generally be described via mathematical functions. Important is the fact that the resulting curve appears different in terms of length and weight and for each species observed. Fish old enough to be measured or exploited usually show a bounded-length growth curve as illustrated in Figure 1a.

Here, the exponential [Fig. 1 b(A)] and sometimes even the linear (B) part of the curve cannot be observed (Fig. 1a,b), because they appear during the very young age of the fish or in fish larval stage. A typical curve of growth in weight shows the typical S-shape and combines three segments (Fig. 1b): an exponential phase (A), a linear phase (B) and a bounded phase (C).

## Material and methods

### Example data set

The example data used in this work are based on length and weight data of turbot (*Scophthalmus maximus*) reared in a marine aquaculture recirculation system (RAS) at 'Gesellschaft für Marine Aquaculture mbH in Büsum' (GMA), Germany. The RAS contained ten identical round tanks of 2.2 m in diameter and a water depth of 1 m. The entire water volume of the RAS was 40 m<sup>3</sup>. Fish were kept at 17°C water temperature over the outgrowing period from the age of 349 to 689 days posthatch. Water parameters were kept stable at  $O_2 \approx 8.2 \text{ mg L}^{-1}$ ,  $NH_4 \approx 0.3 \text{ mg L}^{-1}$ ,  $NO_2^- \approx 2.5 \text{ mg L}^{-1}$  and salinity  $\approx 29\%$ . Fish were fed a special turbot feed, 'Aller 505' (Aller Aqua, Golßen, Germany). All fish were hand-fed once a day on 5–6 days a week. During the outgrowth, fish were ranked in size-graded groups. Pellet size and stocking rate were continuously adjusted to actual size of the fish and common production standards. The data were recorded between 2009 and 2010. A total of  $\approx 1500$  fish were measured frequently during a fattening period of 340 days. Growth data are expressed as standard length (length without caudal fin) and total wet life weight. For this review, growth data in length and weight of 150 female fish were chosen randomly (e.g. Fig. 2, Table 1).

### Calculating growth and goodness of fit

All calculations of growth were performed using the open source software R (R Development Core Team 2013, [www.r-project.org](http://www.r-project.org)).

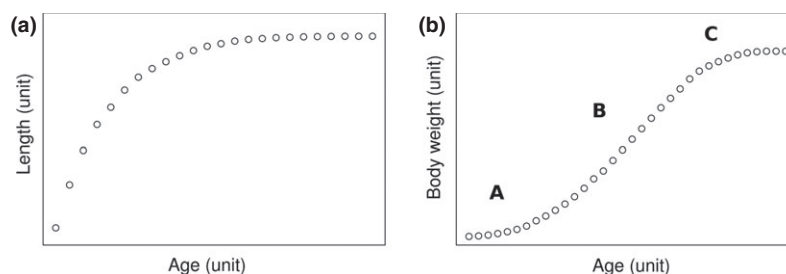


**Figure 1** Typical bounded growth curve of length (a) and S-shaped curve on weight (b) showing an exponential segment (A) a linear segment (B) and a bounded segment (C).

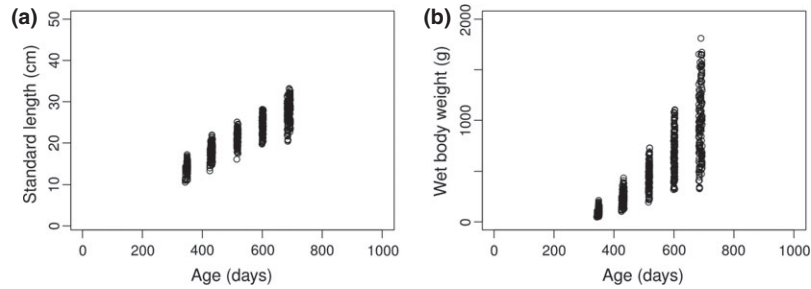


**Figure 2** Standard length (a) and total wet weight (b) of female Turbot;  $n = 150$ .

**Table 1** Mean female turbot length (cm) and weight (g)  $\pm$  Standard deviation (SD) at exact age (days)

| Age (days) | Length (cm) $\pm$ SD | Weight (g) $\pm$ SD |
|------------|----------------------|---------------------|
| 349        | 14.3 $\pm$ 1.33      | 121 $\pm$ 32.9      |
| 431        | 18.3 $\pm$ 1.64      | 253 $\pm$ 68.0      |
| 517        | 21.6 $\pm$ 1.71      | 459 $\pm$ 119.1     |
| 601        | 24.7 $\pm$ 2.15      | 700 $\pm$ 204.5     |
| 689        | 27.6 $\pm$ 2.98      | 980 $\pm$ 354.2     |

Calculations of all nonlinear growth models were performed via nonlinear least square using the Levenberg–Marquardt algorithm for nonlinear regression.

Goodness of fit is expressed by the coefficient of determination ( $R^2$ ) and mean percentage deviation (MPD %) in all cases. For nonlinear models, also the residual standard error (RSE) and corresponding degrees of freedom (DF) are given. Further, we calculated the Akaike information criterion (AIC) for model evaluation.

All functions are extrapolated over a time interval of 1–1000 days to illustrate the shape of the curve generated by the function. This way we can show the differences between each function and the possibility of exact and most realistic prediction of fish growth in aquaculture under the use of the best-fitting function.

## Growth rates

### Absolute growth

One of the quickest, mathematically simplest and frequently used methods in describing growth is the absolute increase in units measured. It is expressed as:

$$\Delta w = w_t - w_i \quad (1)$$

where  $w_t$  is the final weight/length and  $w_i$  is the initial weight/length. This calculation is used simply on harvesting and stocking data. In our example from day 349 to 689, growth was:

$$27.6 \text{ cm} - 14.3 \text{ cm} = 13.3 \text{ cm}$$

or respectively:

$$980 \text{ g} - 121 \text{ g} = 859 \text{ g}$$

Without a relation to time, this is very shallow and insufficient information. Therefore, the time frame is included in the absolute growth rate:

$$\text{AGR} = \frac{w_t - w_i}{t} \quad (2)$$

where  $t$  is time (in our example the fattening period in days). The calculation for the example data set is:

$$\frac{27.6 \text{ cm} - 14.3 \text{ cm}}{340} = 0.04 \text{ cm/day}$$

or respectively:

$$\frac{980 \text{ g} - 121}{340} = 2.5 \text{ g/day}$$

For our example data set, the corresponding  $R^2$  is 0.994123 for length with an MPD of 2.06%. For weight application, the  $R^2$  is 0.985871 and MPD is 11.27%.

To report growth in aquaculture Equation (2) on the basis of grams per day, the calculation mentioned above (Hopkins 1992) is commonly used. Even being widely accepted as one of the standards when reporting growth, the absolute growth rate implies an often underestimated systematic error, which can be easily revealed by graphing it into a data set (Fig. 3). As shown, the absolute growth rate relies on a linear relationship between unit and time. Therefore, in a typically bounded growth curve of fish length, all intermediate data are underestimated. In terms of weight, it is even more precarious. As the typical weight curve includes a point of inflection (POI), previous intermediate data will be overestimated and future data points will be underestimated, dependent on the exact position of the POI within the curve. Our data set is arranged before reaching the POI; therefore, all intermediate data are overestimated by the AGR, resulting in a large MPD. Nevertheless, the AGR can adequately describe short segments of curves and be therefore used in correspondent studies.

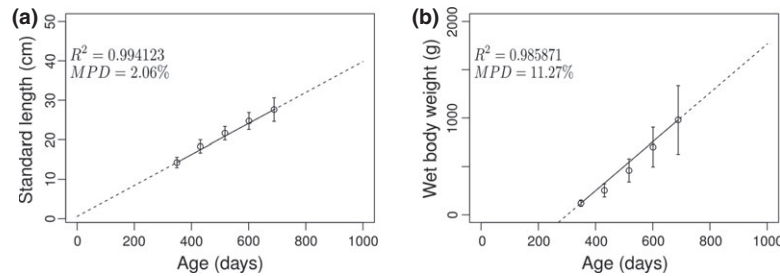


**Figure 3** Absolute growth rate of length (a) and weight (b). Solid lines show interpolated values during the experiment. Dotted lines are modelled extensions (extrapolation) of these. Notice that in length (a) all intermediate data are underestimated, while in weight (b) they are overestimated.

#### Relative growth rate

The relative growth rate (RGR) is mathematically based on the absolute growth rate. It displays the absolute increase in relation to the initial weight/length and is reported as percentage increase over time. Therefore, it is constructed as Equation (1), being additionally divided by the initial weight/length and multiplied by 100. Accordingly, the result is presented in percentage increase:

$$\text{RGR} = \frac{w_t - w_i}{w_i} \times 100 \quad (3)$$

For our example data set of 150 female turbot, we can calculate the length as:

$$\frac{27.6 \text{ cm} - 14.3 \text{ cm}}{14.3} \times 100 = 93.5\% \text{ in 340 days}$$

We can state that the fish grew approximately 93% in 340 days. In terms of weight, we can calculate:

$$\frac{980 \text{ g} - 121 \text{ g}}{121 \text{ g}} \times 100 = 709\% \text{ in 340 days}$$

Fish gained approximately 709% of their initial weight in 340 days. Of great importance is that the calculated values refer strictly to the time it was calculated for. It cannot be easily converted to any other time period (Hopkins 1992). It cannot be stated that 709%/340 days = 2.09%/day.

#### Instantaneous growth rate

The instantaneous growth rate (IGR) relies on the absolute growth rate but instead of calculating the absolute values, it uses the natural logarithm:

$$\text{IGR} = \frac{\log(w_t) - \log(w_i)}{t} \quad (4)$$

where log is the natural logarithm. All other letters are specified as in the previous equations.

#### Specific growth rate

In analogy to the conversion between the absolute growth rate and the relative growth rate, the instantaneous growth

rate can be transferred into the specific growth rate (SGR) by being multiplied by 100. Its results are given in percentage increase per day, which is why it is a more flexible method than the RGR. Accordingly we get:

$$\text{SGR} = \frac{\log(w_t) - \log(w_i)}{t} \times 100 \quad (5)$$

For our example data set in length, we calculate:

$$\frac{\log(27.6 \text{ cm}) - \log(14.3 \text{ cm})}{340} \times 100 = 0.19\% \text{ per day}$$

giving an  $R^2$  value of 0.970866 and MPD value of 5.04%.

For weight we calculate:

$$\frac{\log(980 \text{ g}) - \log(121 \text{ g})}{340} \times 100 = 0.6\% \text{ per day}$$

giving an  $R^2$  value of 0.967807 and MPD value of 13.37%.

Percentage growth per day is practical, when comparing groups of fish in short-term and nutrition experiments. In terms of weight, the SGR might even produce good fitting results for young fish, because their gain in weight is still in the exponential phase of the curve (e.g. Fig. 1). Even though the SGR is established in practical use, an exponential function is the mathematically most imprecise function, which is clarified by low  $R^2$  values and large MPD (Fig. 4). Long-term data or data over different life stages can therefore not be reflected satisfactorily.

It is obvious that the SGR is unable to be used as a model for any predictions about further or previous growth of the fish. All intermediate data will be underestimated. Further data will be overestimated, as well as previous data.

#### The thermal-unit growth coefficient

The theory of the thermal-unit concept dates back to the 18th century. For exact historical processing and applications, we would like to refer the reader to Dumas *et al.* (2010). In this context, it is important to mention that the thermal-unit growth model is an approach of Canadian

scientists to calculate the growth of salmonids in culture. Iwama and Tautz (1981) attempted a general easy-to-use growth model to predict growth as a function of initial body weight ( $w_i$ ), time (days) and temperature ( $^{\circ}\text{C}$ ) being originally expressed as:

$$w_t^{0.33} = w_i^{0.33} + \left(\frac{T}{1000}\right)t \quad (6)$$

where  $w_i$  is initial weight/length,  $w_t$  is final weight/length,  $T$  is temperature in  $^{\circ}\text{C}$ , and  $t$  is time in days. As for most round fish, a weight ( $W$ ) and length ( $L$ ) relationship of  $W \approx L^3$  can be assumed; the function can easily be converted to length (Iwama & Tautz 1981; Jobling 2003). The reader will notice the basic form of a linear equation ( $y = mx + b$ ), and truly,  $W^{0.33}$  and corresponding  $L$  are linear with time (Iwama & Tautz 1981).

By rearranging the formula, the model can be used for weight/length prediction, time prediction and temperature prediction (Iwama & Tautz 1981). As this paper focuses on size prediction, we calculate on the basis of our data set a length of:

$$14.3 \text{ cm} + \left(\frac{17^{\circ}\text{C}}{1000} \times 340\right) = 20 \text{ cm}$$

and a weight of:

$$\left(121 \text{ g}^{0.33} + \left(\left(\frac{17^{\circ}\text{C}}{1000}\right) \times 340\right)\right)^3 = 1234 \text{ g}$$

The results underestimate the measured length of 27.6 cm by 27.5% and overestimate the measured weight of 980 g by 26% (see Discussion).

The model was later modified by Cho (1992) introducing the thermal-unit growth coefficient (TGC) (Eqn 7), which is calculated in relation to degree-days ( $T \times t$ ) (Jobling 2003; Dumas *et al.* 2010). It can be seen as an attempt to improve the SGR (and the corresponding serious deficiency of using the natural logarithm of body size and the corresponding exponential form of the generated curve), by

taking the exponent of 1/3 power (Cho 1992) and bringing it into relation to water temperature, leading to a much less powerful exponential curve (Fig. 5b) (e.g. Kleiber 1975; Iwama & Tautz 1981). In terms of length, it results in a linear relationship between  $L$  and time due to the already mentioned weight/length relationship of  $W \approx L^3$  for round fish. The results are not expressed in percentage increase but as a unit-independent growth coefficient (growth rate), resulting in comparable numbers for fish of various sizes and at various temperatures (Iwama & Tautz 1981). Mathematically, it is expressed as:

$$\text{TGC} = \frac{w_t^{1/3} - w_i^{1/3}}{\text{temp.}(^{\circ}\text{C}) \times \text{days}} \quad (7)$$

where  $w_t$  is the final weight/length,  $w_i$  is the initial weight/length, and temp. ( $^{\circ}\text{C}$ ) is the water temperature in  $^{\circ}\text{C}$  (Cho 1992). Accordingly, we calculated for our example data set a TGC value of:

$$\frac{27.6 \text{ cm} - 14.3 \text{ cm}}{17^{\circ}\text{C} \times 340} = 0.0023$$

This calculation results in the same linear graph as the AGR. Accordingly, the  $R^2$  value and the MPD are the same:  $R^2 = 0.994123$  and MPD = 2.06%.

For weight we calculate a TGC value of:

$$\frac{(980 \text{ g}^{1/3}) - (121 \text{ g}^{1/3})}{17^{\circ}\text{C} \times 340} = 0.00086$$

giving an  $R^2$  value of 0.993926 and an MPD value of 5.51%.

Cho (1992) pointed out that the TGC values and the growth rate are species specific and influenced by several environmental factors, such as nutrition and husbandry. Therefore, it is of great importance to calculate facility-specific TGC values for each species under certain conditions, in order to make reliable prediction.

Considering the above, the TGC can be used for growth modelling using the equations:

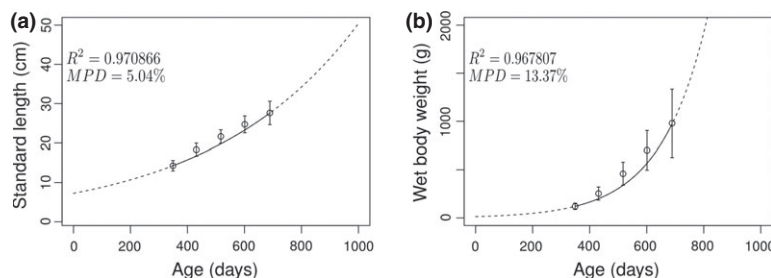


**Figure 4** SGR applied on length data (a) and weight data (b). Notice that all intermediate data are underestimated. Future values will be overestimated, as well as previous values.

$$l_t = [l_i + (\text{TGC} \times \text{temp.} (^{\circ}\text{C}) \times \text{days})] \quad (8)$$

$$w_t = [w_i^{1/3} + (\text{TGC} \times \text{temp.} (^{\circ}\text{C}) \times \text{days})]^3 \quad (9)$$

Its application and the generated shape of the TGC curve are shown in Figure 5.

### Nonlinear growth models

#### The logistic function

The logistic function (Verhulst 1845) is a very common but also very basic form of a sigmoid function. Due to its simplicity, it finds wide application but obtains strong limitation by its mathematical background. Originally, the function was developed to study population growth. Its original form is expressed by the formula:

$$P_{(t)} = \frac{1}{1 + e^{-t}} \quad (10)$$

where  $P_{(t)}$  is the dependent variable (originally  $P$  stands for population; in our case it expresses length or weight),  $e$  is the Euler's number (base of the natural logarithm), and  $t$  is time.

Due to this simple setting, the inflection point of the curve is always set in the middle; both sides are arranged mirror-inverted. The logistic curve is always symmetric. Therefore, the POI has to be determined, as well as the upper asymptote and the growth rate.

To be used for growth calculation, the formula is set to:

$$y_{(t)} = \frac{a}{1 + \left(\frac{b-t}{c}\right)} \quad (11)$$

where  $y_{(t)}$  represents the dependent variable at time  $t$ ,  $a$  is the upper asymptote of the curve,  $b$  represents the time at the inflection point, and  $c$  is the growth rate and scaling parameter of the  $y$ -axis. The inflection point occurs at  $t = \ln(b)/c$ , when  $y = a/2$ .

The parameters were estimated as:

$a = 33.57$  cm, respectively 1414.57 g

$b = 402.77$ , respectively 600.43

$c = 188.97$ , respectively 109.99

Despite its mathematical simplicity, the logistic function provides a much better fit to the data than any of the functions discussed before (Fig. 6) and provides reasonable fit to all intermediate data.

#### The Gompertz function

Like the logistic function, the Gompertz function (Gompertz 1825) is also a sigmoid-shaped saturation function (Fig. 7). In comparison with the logistic function, the Gompertz function is an asymmetric curve with the POI not set in the middle of the curve. It contains three parameters describing the shape of the curve. Its formula is expressed as:

$$y_{(t)} = ae^{\{be^{(\alpha t)}\}} \quad (12)$$

where  $y_{(t)}$  is the dependent variable at time  $t$ ,  $a$  is the upper asymptote,  $b$  sets the  $y$  displacement, and  $c$  is the growth rate scaling the  $y$ -axis. Again,  $e$  is the Euler's number. The inflection point occurs at  $t = (\log b)/c$ , when  $y = a/e$ .

Parameters of the curve were estimated as:

$a = 37.17$  cm, respectively 2531.92 g

$b = 3.1085$ , respectively 10.0482

$c = 0.9966$ , respectively 0.9966

#### Von Bertalanffy growth function (VBGF)

The von Bertalanffy growth function (Von Bertalanffy 1934) is probably the most commonly used growth model in fishery biology. It has two specific terms, one for length application and one for weight application, based on the typical forms of these growth curves (see Figs 1, 2). Therefore, it can reflect each data set more precisely than any of the functions discussed before (Fig. 8), whereas the same function is used for both applications.

The specific form for calculating length is expressed as:

$$l_{(t)} = L_{\text{inf}}(1 - e^{-k(t-t_0)}) \quad (13)$$

where  $l_{(t)}$  is the expected length at a given time ( $t$ ),  $L_{\text{inf}}$  is the asymptotic length,  $k$  is the growth coefficient of the curve, and  $t_0$  sets the point where the curve intersects the  $x$ -axis. The parameters can be calculated via linear regres-

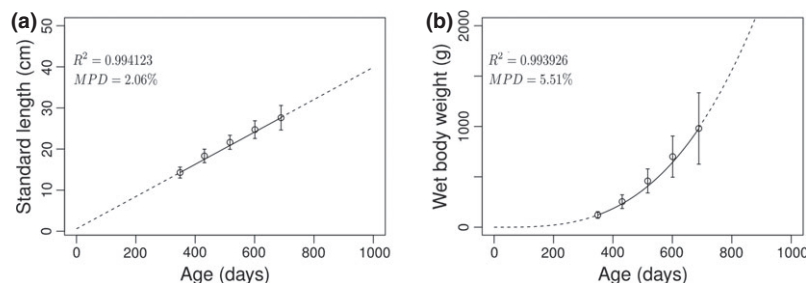


**Figure 5** TGC applied on length data (a) and weight data (b). Notice the analogy of the TGC length application and the AGR length application.

sion, either by Gulland and Holt plot or Walford plot, or by nonlinear least squares, which provides best results.

For calculating weight, it is expressed as:

$$w_{(t)} = W_{\text{inf}}(1 - e^{(-k(t-t_0))})^b \quad (14)$$

where  $w_{(t)}$  is the weight at a given time ( $t$ ) and  $W_{\text{inf}}$  is the asymptotic weight.  $b$  is the slope of the weight/length relationship. It is expressed as:  $W = aL^b$ . All other parameters are used simultaneous with the ones for length application.

The parameters of the function were estimated as:

$L_{\text{inf}}$ : 36.62 cm, respectively  $W_{\text{inf}}$ : 5552.51 g

$k$ : 0.3056, respectively 0.5366

$t_0$ : 0.1866, respectively 0.3514

$b$ : 23.86

*A flexible nonlinear model:*  $y_{(i)} = ae^{-b((t_i-c)/t_i)}$

Kanis and Koops (1990) successfully tested a flexible nonlinear model on growth, daily gain and food intake on different breeds of pigs. We choose this model because of its easy and flexible appliance and interpretable biological parameters (Kanish & Koops 1990). The function represents an intermixture of a classical growth rate, using specific ages in the data set ( $t_i$ ) for calculation, and a growth model, using three parameters to characterize the shape of the curve. It has not been tested on fish growth data yet.

The function of the model is expressed as:

$$y_{(i)} = ae^{-b((t_i-c)/t_i)} \quad (15)$$

where  $y$  is the dependent variable (length or weight),  $e$  is the base of the natural logarithm, and  $t_i$  sets the time frame;  $a$ ,  $b$  and  $c$  are the parameters of the function. This function can provide several different types of curves (e.g. bounded, exponential, U-shaped, S-shaped) (Kanish & Koops 1990) and can therefore be applied on length and weight data without any modification (Fig. 9).

We estimated the three parameters to be:

$a = 40.2581$  cm, respectively 4845.87 g

$b = -0.00028$ , respectively  $-0.00066$

$c = 395.2502$ , respectively 1368.87

#### The Schnute function

Unlike the logistic and the Gompertz function, the Schnute growth model (Schnute 1981) (Fig. 10) provides four parameters to describe the shape of the curve. But unlike the Bertalanffy function, it has no specific application for length and weight data. All data are processed by the same mathematical term. It also includes two data-specific age terms ( $t_1$  and  $t_2$ ) as the Kanish function does, which are set by the data. It also includes two corresponding size parameters ( $y_1$  and  $y_2$ ). Thus, it combines terms of application of the VBGM/Gompertz model and the Kanish function and is

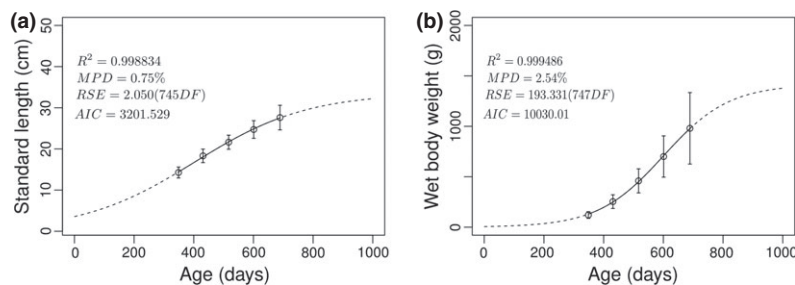


**Figure 6** The Logistic function applied on length data (a) and weight data (b).

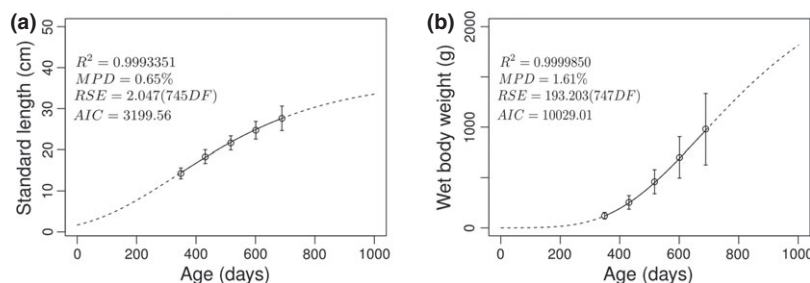


**Figure 7** The Gompertz function applied on length data (a) and weight data (b).

therefore also very flexible. In its notation, several traditional growth models are incorporated as special cases (Bear *et al.* 2010). It can be expressed by four cases:

$$\text{1st } y_{(t)} = \left\{ y_1^b + (y_2^b - y_1^b) \left[ \frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2-t_1)}} \right] \right\}^{1/b} \quad (16)$$

when  $a \neq 0$  and  $b \neq 0$

Here,  $y_{(t)}$  is the dependent variable at time  $t$ ,  $t_1$  is the first specific age in the data set, and  $t_2$  is the last specific time in the data set.  $y_1$  is the corresponding unit ( $y_t$ ) at age  $t_1$ , and  $y_2$  is the corresponding unit ( $y_t$ ) at age  $t_2$ .  $a$  is the constant relative rate of relative growth rate ( $\text{days}^{-1}$ ), and  $b$  is incremental relative rate of relative growth rate.

$$\text{2nd } y_{(t)} = y_1 e^{\{\ln(y_2/y_1)[(1-\exp(-c(t-t_1)))/(1-\exp(-c(t_2-t_1)))]\}} \quad (17)$$

when  $a \neq 0$  and  $b = 0$

$$\text{3rd } y_{(t)} = \left[ y_1^b + (y_2^b - y_1^b) \left( \frac{t - t_1}{t_2 - t_1} \right) \right]^{1/b} \quad (18)$$

when  $a = 0$  and  $b \neq 0$

$$\text{4th } y_{(t)} = y_1 e^{\ln(y_2/y_1)[(t-t_1)/(t_2-t_1)]} \quad (19)$$

when  $a = 0$  and  $b = 0$

Parameters of the curve were estimated as follows:

$y_1 = 14.27$  cm, respectively 120.57 g

$y_2 = 27.63$  cm, respectively 980.08 g

$a = -0.67$ , respectively 1.16

$b = 2.79$ , respectively 0.04

## Discussion

The AGR is a quick and easily applicable way to classify growth. It is widely accepted for comparing results in nutrition and growth studies. It can also produce satisfying results when being used in the linear segment of the growth curve (Fig. 1b) or on short-trail experiments. It is unable to describe the growth during the entire lifespan of an organism or long-term studies that do expand over more than one growth phase. Being applied on length data, all intermediate data will always be underestimated. In weight all intermediate data will be overestimated up to the POI. Afterwards, all intermediate data will be underestimated. It must not be used for prediction of further or previous growth.

The RGR sets growth in relation to the initial size. It is also a reasonable way for growth comparison studies, e.g. when different individuals of the same initial size are studied with different treatments. As it also relies on a linear relationship between time and unit, it shows the same graph as the AGR when being displayed. Receiving relative percentage deliverables, the relative growth rate is well suited of comparison nutrition studies. A big advantage is based in its construction, whereby it can also be used in

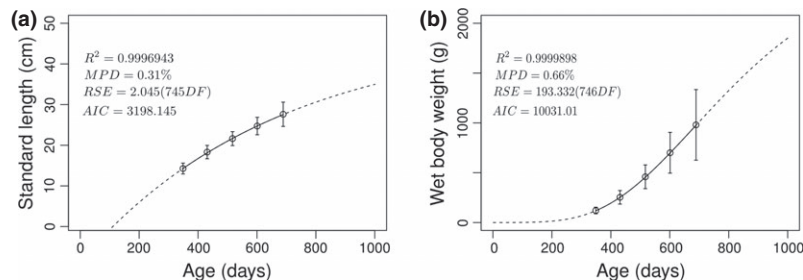


**Figure 8** The VBGF applied to length data (a) and weight data (b). Notice the ideal-like (bounded) shape of the length application.

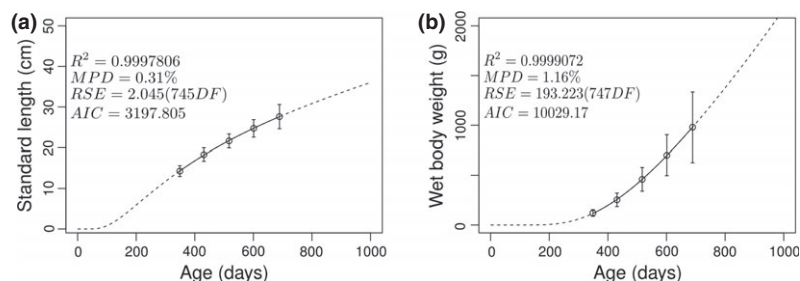


**Figure 9** The non-linear model:  $y_{(t)} = ae^{-b((t-t_1)/t_1)}$  applied on length data (a) and weight data (b).

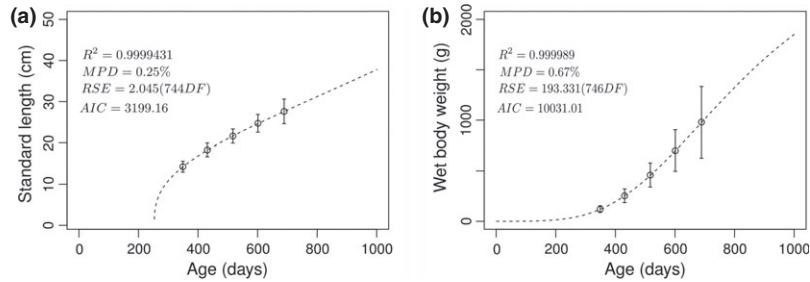


**Figure 10** The Schnute growth model applied on length data (a) and weight data (b).

comparison on fish with different initial sizes (Hopkins 1992).

Although widely accepted as the standard method, we could clarify that the SGR is the mathematically most unsuitable function to describe fish growth when using both long- and short-term data. Due to its exponential background, it must underestimate all intermediate data points. Its exponential form also grossly overestimates predicted body weight greater than the final body weight (Cho 1992). For sure, the assumption of continually exponential growth in fish can be stated incorrect (Dumas *et al.* 2010). The obvious strength lies in its easy application and comparability of its results. Nevertheless, aquaculturists should consider using the absolute growth rate or the TGC, which are both easy to apply and achieve better prediction results and better fit to intermediate data. Results are equally simple to compare and to interpret. The disadvantage of both functions (AGR and SGR) is that comparison is only possible if fish are exactly of the same age, because the functions speculate the natural rhythm of growth of fish during different life stages, which is not the case in the TGC.

Designed for salmonid growth in hatcheries, the thermal-unit growth coefficient has been used intensively on such species (Cho 1992; Dumas *et al.* 2007), but has recently been applied to other aquaculture species such as sea bream (Jauralde *et al.* 2013), where it can gain reasonable results in growth prediction. Its popularity is basically due to its easy application (Jobling 2003). The possibility of predicting growth of different-sized fish reared at different temperatures makes the model very flexible and fulfils the demands of many practical users. But, cautionary has to be paid when the model is applied to various temperature scenarios, because of the dome-shaped curve of growth rate vs. temperature (e.g. Jobling 2003), when temperature is too far of the optimal growing conditions (Dumas *et al.* 2010). This may implant a strong systematical error that may lead to serious prediction errors (Jobling 2003). For our example data set, the model gains strong limitations, because turbot and generally flatfish do not fit into growth and proportion schemes, implied by the model ( $W \approx L^3$ )

(Arfsten *et al.* 2010), leading to increased prediction errors. For general use of flatfish, the model exponent should be adjusted, according to the method implemented by Iwama and Tautz (1981). Further attention needs to be paid to intermediate data, which will be over- or underestimated because  $L$  and  $W^{0.33}$  are linear with time.

Originating from population studies, the logistic function is a three-parameter model that describes a curve with a perfect S-shaped character. It can be seen as a 'prototype' of S-curves, being perfectly symmetric. As the ideal curve of fish growth in length describes a bounded curve, it is unfavourable to use a function that mathematically provides a POI and has an S-shape. In contrast, it is obvious that a perfect S-curve could adequately describe fish growth in weight because growth in weight shows a strong S-shaped character. Due to its symmetric form, it gains strong limitations from the timescale of the data set, because growth curves are often skewed to the right (Kanis & Koops 1990). When the data set contains only early stages of growth, the asymptote will be set far too low. Simulated future data will therefore be estimated very low, as shown on the calculation of our example data set (asymptote = 33.57 cm, respectively, 1414.57 g) which does not fit the biological growth trajectory of turbot. However, previous data can be simulated appropriately. The logistic growth function can gain very good fit to weight data and even provide best fit to about 25% of tested fish species in length (e.g. Katsanevakis & Maravelias 2008).

The Gompertz function or Gompertz curve is also an asymptotic three-parameter growth model. In contrast to the logistic function, it is asymmetric. Therefore, it is more flexible than the logistic function and can provide better fit to given data (Figs 6, 7). Due to its mathematical construction, it also always contains a POI and is therefore very limited when being applied on length data. Though, it can provide very good fit to length data of several elasmobranchs and bony fish species (e.g. Katsanevakis & Maravelias 2008) and even better to weight data and is therefore justifiably one of the most frequently used functions for the calculation of fish growth in weight. The estimations of the

asymptotes are more realistic in biological terms as they are in the logistic model (species and data specific). An asymptotic length/weight of 37.17 cm, respectively, 2531.92 g, seems realistic in terms of SL but not of body weight.

The VBGF is presumably the most often used growth model in fishery science. It has gained serious interest over the last decades and has been tested on numerous fish species, as well as on crustaceans and molluscs. It obtains two specific applications, one for length and one for weight data. Because of its wide application, it is often used *a priori* (Katsanevakis & Maravelias 2008; Baer *et al.* 2010) before even testing other, maybe more suitable models.

Its length application (3-parametric) does not include a mathematically defined POI. Therefore, it can gain very good fit to length data of many fish species. This is where it finds most application, and this is its true strength. For weight application, a fourth parameter is attached. This parameter ( $b$ ) refers to the length/weight relationship which is expressed by the formula:  $W = aL^b$  (often  $a$  is fixed as 1 and using the VBGF,  $a$  is set as 1 and  $b$  is fixed as 3 in order to meet the ideal weight/length relationship of  $W \approx L^3$ ), and indeed, for many round fish species,  $b$  can be estimated close to 3 when calculated as relation between standard weight and total length (length from tip of snout to end of caudal fin). When calculating with standard length,  $b$  correspondingly changes in value. As the parameter  $b$  is additionally attached to the formula to gain an S-shape and a POI a certain inaccuracy can be foreseen, particularly if  $b$  is fixed to 3 in advance. It is therefore important to test a variety of S-shaped curves because the chances of gaining better fit to the data by some other function is high. The asymptote of the von Bertalanffy function  $L_{\text{inf}} = 36.62$  cm, respectively,  $W_{\text{inf}} = 5552.51$  g can be assumed realistic (e.g. Hohendorf 1966; Krüger 1973). The length asymptote is here very close to the one estimated by the Gompertz function. If two different functions provide such close results, which can both be confirmed by other data (e.g. wild fish), it supports the assumption of a biological asymptote within this range. Further, the growth coefficient ( $k$ ) of the function can be used for interpretation and comparison. Species specifically, it usually provides values between 0 and 1. Our estimated  $k$ : 0.3056 for length, respectively, 0.5366 for weight are above those provided in the literature of wild turbot (Hohendorf 1966), being influenced by breeding and the strong growth promotion in RAS aquaculture. An approach to gain more comparability is to fix the asymptote parameter to an evaluated species and system-specific value, as well as the  $t_0$  value. Therefore, only the growth parameter  $k$  varies during the nonlinear regression procedure and can be used to detect impact of treatments on growth patterns.

The flexible three-parametric Kanis model was originally designed to calculate daily weight gain, daily food intake

and food efficiency (Kanis & Koops 1990) as a matter of live body weight of growing pigs. Assuming that food intake decreases proportionally as the animals grow heavier, the resulting curve has a bounded shape, as it can be observed in fish growth in length as a matter of time. The function can therefore be adequately used to calculate fish growth in length and can even gain similar or better fit than the VBGF. As the function is very flexible in its application, it can assume several different shapes including exponential and S-shape. It can therefore also be used for calculation of fish growth in weight as shown for our example data set. Here, it can also produce very good fit, almost similar to the logistic or Gompertz function. Whereas it does not include a mathematically fixed POI, it can also adequately describe short segments of a growth curve or the exponential phase of juvenile fish. Unlike the VBGF it cannot produce negative values, the Kanis model will therefore predict zero growth until the first positive value. Kanis and Koops (1990) set a high value on biological interpretability of the parameters of their equation. For further information, the reader is referred to Kanis and Koops (1990).

The versatile, four-parametric Schnute growth model can also be used for a wide range of applications, including length and weight calculation of fish under the use of the same equation, and without any specific modification of the function. As mentioned, it includes two data-specific age terms ( $t_1$  and  $t_2$ ) like the Kanis function does, but it also includes two corresponding size parameters ( $y_1$  and  $y_2$ ). Thus, it combines terms of application of the VBGM/Gompertz model and the Kanis function, which not only makes it very flexible but also relates it mathematically very close to the data, resulting in a very good fit. For our example data set, the Schnute function performed best in terms of MPD when being applied on length data and gained second place in weight application. When being compared by RSE, it has about the same goodness of fit as the famous VBGM has, pointing out its great potential for aquaculture use. In terms of shape, the Schnute function was not able to make realistic prediction of previous growth of fish in length, but for future growth which is of major importance. In weight application, there was no visible difference in form between the Gompertz, Bertalanffy and Schnute functions noticeable in our 1000-day simulation, but the asymptotic values differ.

## Conclusion

Growth is an ongoing process, influenced by many internal and external factors, resulting in individual and species-specific curves with different mathematical properties during different life stages.

Under the stable conditions of an RAS, when food is no limiting factor, nonlinear growth models calculating growth as a function of age can achieve great match to col-

lected data. They can therefore provide an attestable basis for future growth simulation. As previously mentioned, the choice of the function is strongly correlated with its considered range of application, the given data set and fish species. In our comparably small example data set, statistical differences between the models were minor, indicating the great individual potential of all functions processed. A priori choice of any of the functions processed can therefore lead to misleading results and conclusions. Dependent on the needs of the application, different evaluation methods are available. Goodness of fit between the model and the data can be expressed by mean percentage deviation, which is reasonable if intermediate data are of great interest. For prediction purposes, attention should not be exclusively paid to the goodness of fit of a certain function, but also the shape of the generated curve as well as the regression parameters to evaluate the best model for a certain data set and application. For scientific model evaluation, the AIC should be considered as well because it compensates for the varying number of parameters between models and enables a more objective view of the quality of the model.

In summary, we can state that when easy comparable results are needed, the AGR and TGC can display results with reasonable fit to intermediate data and should be considered as an alternative to the SGR, whereas the TGC can also be used for basic growth prediction. If a more precise model is needed, evaluation of a nonlinear function via multimodel inference shows a promising way to find the most suitable model for each species, set of data and needed form of application.

## Acknowledgement

The authors like to thank the German Federal Office for Agriculture and Food for financing this project.

## References

- Arfsten M, Tetens J, Thaller G (2010) Die Nutzung einfach erfassbarer Körpermerkmale zur Beurteilung von Leistungsparametern beim Steinbutt (*Psetta maxima* L.). *Züchtungs-kunde* **82**: 371–386.
- Baer A, Schulz C, Traulsen I, Krieter J (2010) Analysing the growth of turbot (*Psetta maxima*) in a commercial recirculation system with the use of three different growth models. *Aquaculture International* **19**: 497–511.
- Brett JR (1979) Environmental factors and growth. *Fish Physiology* **8**: 599–675.
- Brody S (1945) *Bioenergetics and Growth*. Reinhold Publishing Corporation, New York.
- Cho CY (1992). Feeding systems for rainbow trout and other salmonids with reference to current estimates of energy and protein requirements. *Aquaculture* **100**: 107–123.
- Dénier C (1990) Comparative study of growth of flatfishes on the west coast of Brittany. *Journal of Fish Biology* **37**: 149–166.
- Dumas A, France J, Bureau DP (2007) Evidence of three growth stanzas in rainbow trout (*Oncorhynchus mykiss*) across life stages and adaptation of the thermal unit growth coefficient. *Aquaculture* **267**: 139–146.
- Dumas A, France J, Bureau D (2010) Modelling growth and body composition in fish nutrition: where have we been and where are we going? *Aquaculture Research* **41**: 161–181.
- FAO (2012). The state of world fisheries and aquaculture 2012. Food and agriculture organization of the United Nations. Report nr 978-92-5-107225-7.
- Gompertz B (1825) On the nature of the function expressive of the law of human mortality. *Philosophical transactions of the Royal Society of London* **36**: 513–585.
- Hernandez-Llamas A, Ratkowsky DA (2004) Growth of fishes, crustaceans and molluscs: estimation of the von Bertalanffy, Logistic, Gompertz and Richards curves and a new growth model. *Marine Ecology Progress Series* **282**: 237–244.
- Hesse R (1927) *Über Grenzen des Wachstums*. Gustav Fischer, Jena.
- Hohendorf K (1966) Eine Diskussion der von Bertalanffy Funktionen und ihre Anwendung zur Charakterisierung des Wachstums von Fischen. *Kieler Meeresforschung* **22**: 70–97.
- Hopkins KD (1992) Reporting fish growth, a review of the basics. *Journal of World Aquaculture Society* **23**: 173–179.
- Imslund AK, Jonassen TM (2003) Growth and age at first maturity in turbot and halibut reared under different photoperiods. *Aquaculture International* **11**: 463–475.
- Imslund AK, Foss A, Alvseike T, Folkvord A, Stefansson SO, Jonassen TM (2007a) Interaction between temperature and photoperiod on growth and feeding of Atlantic cod (*Gadus morhua*): possible secondary effects. *Canadian Journal of Fisheries and Aquatic Sciences* **64**: 239–248.
- Imslund AK, Schram E, Roth B, Schelvis-Smit R, Kloet K (2007b) Growth of juvenile turbot *Scophthalmus maximus* (Rafinesque) under a constant and switched temperature regime. *Aquaculture International* **15**: 403–407.
- Iwama GK, Tautz AF (1981) A simple growth model for salmonids in hatcheries. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 649–656.
- Jauralde I, Martínez-Llorens S, Tomás A, Ballestrazzi R, Jover M (2013) A proposal for modelling the thermal-unit growth coefficient and feed conversion ratio as functions of feeding rate for gilthead sea bream (*Sparus aurata* L.) in summer conditions. *Aquaculture Research* **44**: 242–253.
- Jobling M (2003) The thermal growth coefficient (TGC) model of fish growth: a cautionary note. *Aquaculture Research* **34**: 581–584.
- Kanis E, Koops WJ (1990) Daily gain, food intake and food efficiency in pigs during the growing period. *Animal Production* **50**: 353–364.
- Karås P, Klingsheim V (1997) Effects on temperature and salinity on embryonic development of turbot (*Scophthalmus*

- maximus* L.) from the North Sea, and comparison with Baltic populations. *Helgoländer Meeresuntersuchungen* **51**: 241–247.
- Katsanevakis S, Maravelias CD (2008) Modelling fish growth: multi-model inference as a better alternative to a priori using von Bertalanffy equation. *Fish and Fisheries* **9**: 178–187.
- Kleiber M (1975) *The Fire of Life. An Introduction to Animal Energetics*. Krieger Pub, Huntington, NY, 453 pp.
- Klinkhardt M (2011). *Aquakultur Jahrbuch 2010/2011*. Fachpresse Verlag, Hamburg, 266 pp.
- Krieter J, Kalm E (1989) Growth, feed intake and mature size in Large White and Pietrain pigs. *Journal of Animal Breeding and Genetics* **106**: 300–311.
- Krüger F (1965) Zur Mathematik tierischen Wachstums. I. Grundlagen einer neuen Wachstumsfunktion. *Helgoländer wiss. Meeresunters* **12**: 78–136.
- Krüger F (1973) Mathematik tierischen Wachstums. II. Vergleich einiger Wachstumsfunktionen. *Helgoländer wiss. Meeresunters* **25**: 509–550.
- López S, France J, Gerrits WJ, Dhanoa MS, Humphries DJ, Dijkstra J (2000) A generalized Michaelis-Menten equation for the analysis of growth. *Journal of Animal Science* **78**: 1816–1828.
- Ma A, Chen C, Lei J, Chen S, Zhuang Z, Wang Y (2006) Turbot *Scophthalmus maximus*: stocking density on growth, pigmentation and feed conversion. *Chinese Journal of Oceanology and Limnology* **24**: 307–312.
- Parks JR (1982) *A Theory of Feeding and Growth of Animals*. Springer-Verlag, Berlin.
- Pütter A (1920) Wachstumsähnlichkeiten. *Pfluegers Arch. Gesamte Physiol. Menschen Tiere* **180**: 298–340.
- Richards FJ (1959) A Flexible Growth Function for Empirical Use. *Journal of Experimental Botany* **10**: 290–301.
- Ricker WE (1979). Growth rates and models. In: Hoar WS, Randall DJ, Brett JR (eds). *Fish Physiology, Volume VIII. Bioenergetics and Growth*, pp. 679–743. Academic Press, New York.
- Rosenlund G, Karlsen Ø, Tveit K, Mangor-Jensen A, Hemre G-I (2004) Effect of feed composition and feeding frequency on growth, feed utilisation and nutrient retention in juvenile Atlantic cod. *Gadus morhua* L. *Aquaculture Nutrition* **10**: 371–378.
- Schnute J (1981) A versatile growth-model with statistically stable parameters. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 1128–1140.
- Slawski H, Adem H, Tressel R-P, Wysujack K, Kotzamanis Y, Schulz C (2011) Austausch von Fischmehl durch Rapsproteinkonzentrat in Futtermitteln für Steinbutt (*Psetta maxima* L.). *Züchtungskunde* **83**: 451–460.
- Springborn RR, Jensen AL, Chang WYB (1994) A variable growth rate modification of von Bertalanffy's equation for aquaculture. *Aquaculture and Fisheries Management* **25**: 259–267.
- Verhulst P-F (1845) “Recherches mathématiques sur la loi d'accroissement de la population” [Mathematical Researches into the Law of Population Growth Increase]. *Nouveaux Mémoires de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles* **18**: 1–42.
- Von Bertalanffy L (1934) Untersuchungen über die Gesetzlichkeit des Wachstums I. *Wilhelm Roux' Arch. EntwMech. Org.* **131**: 613–653.
- Von Bertalanffy L (1938) A quantitative theory of organic growth (Inquiries on growth laws II). *Human Biology* **10**: 181–213.